Distribution, utilization and management of the extra-limital common warthog (*Phacochoerus africanus*) in South Africa

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Declaration

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Notes

This thesis is presented in the format prescribed by the Department of Conservation Ecology and Entomology, Stellenbosch University. The structure is in the form of one or more research chapters (papers prepared for publication) and is prefaced by an introduction chapter with the study objectives, followed by a literature review chapter and culminating with a chapter for elaborating a general discussion and conclusions. Language, style and referencing format used are in accordance with the requirements of the American Psychological Association. This thesis represents a compilation of manuscripts where each chapter is an individual entity and some repetition between chapters has, therefore, been unavoidable.

Results from this dissertation that have been published in the following journals:

- Matthee, S., Swanepoel, M., Van der Mescht, L., Leslie, A. J. & Hoffman, L. C. (2013). Ectoparasites of a non-indigenous warthog population, *Phacochoerus africanus*, in the Free State Province, South Africa. *African Zoology, 48*, 259-265.
- Swanepoel, M., Leslie, A. J. & Hoffman, L. C. (2014). Carcass yield of common warthog (*Phacochoerus africanus*); influence of season and sex. *South African Journal of Wildlife Research, 44,* 179-188.
- Swanepoel, M., Leslie, A. J. & Hoffman, L. C. (2016). Comparative analyses of the chemical and sensory parameters and consumer preference of a semi-dried smoked meat product (cabanossi) produced with warthog (*Phacochoerus africanus*) and domestic pork meat. *Meat Science*, *114*, 103–113. doi:10.1016/j.meatsci.2015.12.002.
- Swanepoel, M., Leslie, A. J., & Hoffman, L. C. (2016). Farmers' perceptions of the extra-limital common warthog in the Northern Cape and Free State provinces, South Africa. *Wildlife Society Bulletin*. doi:10.1002/wsb.617.

Results from this dissertation that have been presented at the following conferences:

- Swanepoel, M., Leslie, A. J. & Hoffman, L. C. (2011). The chemical composition of warthog (*Phacochoerus africanus*) meat. 7th International Wildlife Ranching Symposium, Kimberley, South Africa; 10-14 October 2011. Poster presentation.
- Swanepoel, M., Hoffman, L. C., Muller, M. M., & Leslie, A. J (2012). Consumer preference of cabanossi made from domestic pig (*Sus scrofa*) and warthog (*Phacochoerus africanus*) meat**.** South African Wildlife Management Association (SAWMA) Symposium, Bela-Bela, South Africa; 16-19 September 2012. Oral presentation.

Summary

In South Africa, the recognition of wildlife as a natural resource has developed into a lucrative game farming industry where wildlife has value for tourism, recreational hunting and commercial hunting, including meat production and live sales. The modern game ranching industry is largely influenced by the demand of tourists and hunters for certain species and a great diversity of species, which has resulted in South Africa having the second highest rate of ungulate introductions globally. The common warthog (*Phacochoerus africanus*) was extra-limitally introduced to various game farms and reserves in the Eastern Cape, Northern Cape and the Free State provinces of South Africa for conservation and game farming purposes. Warthogs are not enclosed by the standard fencing used on agricultural lands and nature reserves, and have become free-roaming in the introduced habitats. The species currently inhabit both private and public lands on which major agricultural activities are practiced in South Africa and as a known agricultural pest, have become a managerial problem in traditional agricultural settings. The meat from hunted warthog carcasses is still relatively under-utilized by hunters and/or the commercial sector likely from a lack of information regarding the safety and preparation of the meat.

The study found that introduced warthogs are simultaneously considered and managed as an agricultural pest and game animal by agricultural producers. This conflicting approach to management results in unethical and unsustainable control practices with undesirable outcomes for both farmers and warthogs. Since the majority of agricultural producers indicated that they would be more likely to utilize the meat if presented with information on its nutritional profile, the study proposed the production and utilization of warthog meat as fresh game meat or processed game meat products as a strategy to purposefully manage introduced warthog populations. There is a general concern that introduced warthogs could be responsible for introducing and transmitting diseases to animals and humans, and the consumption of warthog meat could cause diseases or parasitic infections in humans. The study found the first record of the tick *Rhipicephalus gertrudae* on warthogs in South Africa to date, while the low abundance of *R. simus* was attributed to the fact that the study area largely fell outside the ticks' preferred distribution range. Overall, the parasite species richness in the host population was low. These results may suggest that introduced warthogs can alter the distribution of parasites, and/or act as host to parasites not previously associated with warthogs. However, although warthogs are able to carry and transmit diseases to animals and humans, there is a lack of documented cases of this occurring in southern Africa outside of disease-controlled areas. In addition, no warthogs culled during this study showed obvious symptoms of diseases or carriers of parasites potentially harmful for human consumption, albeit this was not explicitly investigated in this study.

The yields and meat quality characteristics of warthogs, and the use of warthog meat in processed products as determined in this study provides evidence that the species can be considered and utilized as a game animal for formal meat production. The overall carcass yields of warthogs were favourable and comparable to those of other wild ungulates, indicating production of warthog meat is economically feasible. Considering the effect of intrinsic factors such as sex and age, age appeared to have a more pronounced effect on the quality characteristics of warthog meat, while adult male warthogs had heavier body weights and higher yields compared to females. The study concluded that warthog meat should be marketed and labelled as whole muscle cuts considering the differences in quality characteristics among skeletal muscles. However, differences between sex, age and among muscles are considered negligible in terms of its nutrition and healthiness as the raw and cooked meat meat is high in protein (~ 20%) and low in fat (~ 2%) with a favourable polyunsaturated to saturated fatty acids ratio (PUFA:SFA) of < 0.45 and omega 6 to omega ratio 3 (ω6:ω3) ratio < 4, which is the recommended ratio for the human diet. However, the *Longissimus lumborum* (LL) muscle from warthogs culled on agricultural lands had a ω6:ω3 ratio > 4 compared to warthogs culled on a game reserve, while warthogs culled on the game reserve had higher levels of arachidonic acid. These differences were attributed to the differences in the regional and seasonal diet of warthogs.

The sensory profile of warthog meat was dominated by pork aroma and flavour and tenderness, and it was proposed that total moisture content is an important factor influencing the sensory profile of warthog meat considering the overall low total fat. The meat was not described as being gamey, which raises the question of whether gamey attributes should be described as ‘associated with game meat’, and its aptness to distinguish among meat from different species. The study found the undesirable aroma and flavour described as “sour/sweaty” was not found only in adult males and was scored higher for juvenile warthogs of both sexes. The use of game meat in processed products could extend the value chain of game meat production, and the study found that warthog meat can be converted to healthy processed products without compromising the sensory attributes associated with the product, while providing further evidence that processes such as curing and smoking is able to reduce or ‘mask’ undesirable flavours. Neither sex nor age ultimately influenced the sensory profile of warthog back bacon produced from the *Longissimus thoracis et lumborum* muscle, which was overall high in total protein (~29%) and low in fat (< 2%) with a favourable fatty acid (FA) profile. The use of warthog meat in a ready-to-eat product known as cabanossi found that warthog and pork cabanossi had similar total protein (26.3% and 24.2%, respectively) contents, while the warthog cabanossi was lower in total fat content (6.9% and 13.7%, respectively), which did not affect consumer preference. Despite the encouraging results found in this study regarding the quality and properties of warthog meat, there are still many research questions regarding the distribution, impacts, utilization and management of warthog populations in South Africa. The study in its entirety provides baseline information pertaining to and influencing warthog yields and meat quality characteristics, and concludes that warthogs can be utilized as a game animal for meat production and utilization, with the benefit of producing an overall lean meat with desirable properties for processing.

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Opsomming

Die erkenning van wild as n natuurlike hulpbron het in Suid Afrika ontwikkel as ‘n aanloklike wildindustrie wat vleisproduksie en lewende verkope insluit. Die moderne wildboerdery word grootliks beinvloed deur die aanvraag van toerisme sowel as die jag van spesifieke spesies, asook ‘n verskeidenhied van ander spesies, wat daartoe gelei het dat Suid Afrika die tweede hoogste voorkoms van die vestiging van hoefdiere in die wereld het. Die algemene vlakvark (*Phacochoerus africanus*) is op klein skaal binne die landsgrense op verskeie wildreservate in die Oos Kaap, Noord Kaap en die Vrystaat gevestig vir wildbewarings- en wildboerderydoeleindes. Vlakvarke word nie binne gehou deur die standaard heinings wat op landbougrond en wildsreservate gebruik word nie, en beweeg vryelik rond in die gebiede waar hulle ingebring is. Die spesie kom tans algemeen op beide openbare en private grond waarop landbou bedrywighede plaasvind, voor, en het as ‘n algemene probleemdier in ‘n bestuursprobleem vir die boere en eienaars ontaard. Die vleis van die die vlakvark wat gejag word is tans nog relatief onbenut deur sowel die jagter as die sakesektor, waarskynlik a.g.v. ‘n gebrek van inligting aangaande die veiligheid en voorbereiding van die vleis.

Hierdie studie het gevind dat vlakvarke as probleemdier sowel as wildspesie deur die landbouers beskou word. Hierdie konflikterende beskouing het uitgeloop op onetiese en onvolhoubare beheermaatreels wat tot onbevredeginde resultate vir beide die boere en die vlakvarke gelei het. Aangesien die meerderheid landbouers aangedui het dat hulle heel waarskynlik die vleis sou gebruik as hulle ingelig kon word oor die voedingswaarde daarvan, stel hierdie studie die produksie en benutting van vlakvarkvleis as vars en geprosesseerde wildsprodukte voor, as ‘n strategie om daardeur doelbewus die vlakvark populasies te probeer beheer. Daar bestaan ‘n algemene bekommernis dat vlakvarke verantwoordelik kan wees vir die bekendstelling en oordrag van siektes na die mens en ander diere en dat die verbruik van die vleis parasitiese infeksies en ander siektes in die mens kan veroorsaak. Die studie bied die eerste dokumentering van die bosluis, *Rhipicephalus gertrudae* wat tot op datum op vlakvarke in Suid Afrika gevind is, terwyl die lae infestasie van *R simus* daaraan toegeskryf kan word dat die studiearea grotendeels buite die bosluis se verkose verspreidingsarea val. Oor die algemeen was die infestasie van ekto-parasiete op die gasheerpopulasie laag. Hierdie bevindings kan daarop dui dat die vlakvarke die verspreiding van parasiete kan verander en/of as gasheer vir parasiete wat voorheen nie met vlakvarke geassosieer is nie, optree. Hoewel vlakvarke daartoe instaat is om siektes te dra en oor te dra, is daar ‘n gebrek aan gedokumenteerde gevalle van die aard in Suid Afrika. Geeneen van die vlakvarke wat vir hierdie studie gebruik is, het enige tekens van ooglopende siektes gehad of dat hulle draers van parasiete is, wat potensiëel gevaarlik vir menslike gebruik is nie. Hierdie aspek is egter nie eksplisiet in die studie ondersoek nie.

Die gebruik en kwaliteit van vlakvarkvleis in geprosesseerde produkte soos vasgestel in hierdie studie voorsien bewyse dat die spesie beskou en benut kan word as 'n jagdier vir formele vleisproduksie. Die algemene uitslag persentasie van vlakvarke was gunstig en vergelykbaar met die van ander hoefdiere wat daarop dui dat die produksie van vlakvarkvleis ekonomies haalbaar is. As die intrinsieke faktore soos geslag en ouderdom in ag geneem word, het ouderdom 'n duidelike effek op die kwaliteit van vlakvarkvleis, terwyl volwasse manlike vlakvarke swaarder geweeg en 'n hoër uitslag persentasie as vroulike diere gehad het. Die studie het ook tot die gevolgtrekking gekom dat vlakvarkvleis gemerk en bemark behoort te word as heel spiersnitte, met inageneming van die verskille in die kwaliteit van die verskillende skeletspiere. Die verskille tussen ouderdom, geslag en tussen spiere word as onbeduidend in terme van die voedingswaarde en gesondheidsvoordele beskou, aangsien die rou en gaar vleis hoog in totale proteien- (~ 20%) en laag in totale vet-inhoud (~ 2%) is met 'n gunstige poliversadigde tot versadige vetsuur verhouding (PUFA:SFA) van < 0.45 en omega 6 tot omega 3 verhouding (ω6:ω3) wat die aanbevole verhoudings vir die menslike dieet is. Die LL spiere van die die vlakvark wat op landbougrond gejag is het egter 'n verhouding van ω6:ω3 > 4 gehad teenoor die wat op 'n wildreservaat gejag is, terwyl vlakvarke wat op die jagreservaat gejag is, hoër vlakke van arachidoniese suur gehad het. Hierdie verskille is toegeskryf aan die verskille tussen die streeks- en seisoenale dieet van die vlakvarke.

Die sensoriese profiel van vlakvarkvleis word gedomineer deur 'n varkvleis-aroma en -smaak, en sagtheid. Die totale voginhoud is 'n belangrike bepalende faktor vir die sensoriese profiel van vlakvarkvleis as die algemene lae vetinhoud in ag geneem word. Die vleis was nie beskryf as tipies wild nie, wat die vraag laat onstaan of wildseienskappe daaraan toegedig of toepaslik gebruik moet word om tussen die vleis van verskillende spesies te onderskei. Die studie het gevind dat die ongewenste aroma en geur wat as "suur/sweterig" beskryf word, nie net in volwasse manlike diere voorgekom het nie en 'n hoër telling is aangeteken vir jong vlakvarke van beide geslagte. Die gebruik van wildsvleis in geprosseseerde produkte kan die waardeketting van wildsvleisproduksie verleng. Die studie het bevind dat vlakvarkvleis tot gesonde geprosseseerde produkte verwerk kan word, sonder om die sensoriese eienskappe wat met die produk geassosieer word, in te boet. Verder word bewys dat prosesse soos die pekel en rook van die vleis die ongewensde geure kan verminder of verbloem. Nie die geslag of ouderdom het die sensoriese profiel van die vlakvarkrugspek wat van die *Longissimus thoracis et lumborum* spier gemaak is, beinvloed nie. Dit was oor die algemeen hoog in totale proteiene (~29%) en laag in vet (< 2%)met 'n gunstige vetsuur (FA) profiel. Met die gebruik van vlakvarkvleis in 'n gereed-om-te-eet produk bekend as cabanossi is bevind dat vlakvark- en varkcabanossi ooreenstemmende totale proteien (26.3% en 24.2%, respectively) inhoud gehad het, terwyl vlakvarkcabanossi laer in vetinhoud (6.9% en 13.7%, onderskeidelik) was, wat nie verbruikersvoorkeure beinvloed het nie. Ten spyte van die bemoedigende resultate wat hierdie studie aangaande die kwaliteit en eienskappe van vlakvarkvleis gevind het, is daar steeds vele navorsingsvrae oor die verspreiding, impak, gebruik en bestuur van die vlakvarkpopulasies in Suid Afrika. Die studie voorsien in sy geheel basiese inligting oor die faktore wat vlakvarkprodukte en -kwaliteit beinvloed en kom tot die gevolgtrekking dat vlakvarke as jagspesie vir vleisproduksie en -gebruik benut kan word, met die voordeel van 'n laevet vleis wat oor positiewe eienskappe vir prosessering beskik.

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Chapter 1
General Introduction

In South Africa, the recognition of wildlife as a natural resource has developed into a lucrative game farming industry where wildlife has value for tourism, recreational hunting and commercial hunting, including meat production and live sales (Van der Merwe & Saayman, 2003). Game viewing is a popular activity for the tourism sector, with reserves and game farms hosting a large variety of species considered charismatic for public enjoyment and education, while 'biltong' and trophy hunting is pursued by local and international hunters generates money from hunting (Van der Merwe & Saayman, 2003, Warren, 2011). The modern game ranching industry is influenced by the demand of tourists and hunters for certain species and a great diversity of species, which has driven the introduction and translocation of wildlife species across farms in South Africa despite, the country's naturally rich in wildlife biodiversity (Barnes & de Jager, 1996, Castley, Boshoff, & Kerley, 2001). As a result, South Africa has the second highest rate of ungulate introductions globally, preceded only by the United States (Spear & Chown, 2009).

The common warthog (*Phacochoerus africanus*) was introduced to reserves and ranches across the country including the former range of the extinct Cape warthog (*P. aethiopicus*). Further introductions onto private game farms-and-reserves followed as the species are considered a charismatic game animal. Conservation authorities allowed the introduction of mammals outside their natural range if the area of introduction was sufficiently fenced to enclose populations, including several provincial and national reserves in South Africa. Warthogs are not contained by standard wire or wire mesh fencing used for farms and reserves to enclose populations, and became free-roaming and able to disperse within the introduced area. Nyafu (2009) determined that introduced warthogs are regarded as a high risk species by agricultural producers in the Eastern Cape province. Warthogs currently inhabit both private and public lands on which major agricultural activities are practiced in South Africa and are a known agricultural pest.

Humans can be considered as a major predator of warthogs as they are heavily hunted in their natural range (Caro, 2005, Wilfred, 2012). The species is simultaneously hunted for damage reprisal and/or for financial gains through meat and trophy hunting, and is therefore part of a unique paradigm where a wildlife species is considered, and subsequently managed, as either a damage-causing or valuable species. Hunting is considered a simple and effective control method for wildlife with the added benefit of producing meat (Parkes & Murphy, 2003), while the formal production of meat from wild animals has been suggested as a low-input, high production alternative to traditional animal husbandry (Van

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Schalkwyk, McMillin, Witthuhn, & Hoffman, 2010, Kiley-Worthington, 2014). Although Hoffman, Muller, Schutte, Calitz, & Crafford (2005) found warthogs are a game meat species regularly consumed in South Africa and South African restaurants, the meat from hunted carcasses is still relatively under-utilized by hunters and/or the commercial sector. Local communities have often rejected warthog meat due to an association with 'boar taint' or 'smelly/tainted' meat, which is commonly considered to only pertain to adult warthog boars. The prevalence of an undesirable flavour could affect overall consumer liking/acceptability of the meat, but there is limited research available on warthog meat regarding overall meat quality, sensory profile and usability in meat processing. Similar to other game species, warthogs have a high dressing percentage, low total intramuscular lipid content, high total protein and moisture content and a favourable fatty acid (FA) profile (Crawford, Gale, & Woodford, 1970, Somers, 1992, Hoffman & Sales, 2007). Game animals are considered superior to domestic livestock regarding carcass and meat quality and generally produce a lean and healthy meat (Hoffman, 2008).

The first objective of this study is to investigate how the current and expanded distribution of warthogs affects the perception and management of warthogs by agricultural producers, and the overall use of warthog meat from hunted/killed warthogs on agricultural lands. The second objective was to investigate the yields and physical, chemical and sensory characteristics of warthog meat regarding the influence of intrinsic factors including sex and age, in order to determine whether warthogs have potential for game meat production and utilization. Furthermore, the study aims to investigate the use of warthog meat in processed meat products as an avenue to expand game meat utilization and the market niche in South Africa. It is envisaged to encourage the production and utilization of warthog meat as fresh game meat or processed game meat products, as a strategy to purposefully manage introduced warthog populations. Game meat consumption contributes towards sustainable wildlife and habitat management, and local food security, while generating an income from a widely available resource (Barnes & De Jager,1996, Poshiwa, Groeneveld, Heitkönig, & Prins, 2013).

In addition, warthogs may carry or be susceptible to a range of different diseases that are potentially transmissible to animals and humans, but there has been limited attention given to the prevalence and risk of disease among free-ranging warthog populations in South Africa. Warthogs are considered the major host of the *Ornithodoros* tick species which is responsible for the transmission and spread of African Swine fever (ASF) in domestic pigs (Penrith, 2009). Therefore, the study also aims to conduct a comprehensive review of these diseases and their associated risks and investigate the ecto-parasites of introduced warthog populations, and conduct an investigation of the ecto-parasites of an introduced warthog population.

To summarize, the study aims to determine how introduced warthogs and their impacts are perceived by farmers and how the species are subsequently managed, while there is also a general concern whether warthogs could be responsible for introducing and transmitting pests and parasites to animals and humans, and that consumption of warthog meat could cause diseases or parasitic infections in humans. Therefore, the study also aims to investigate the ectoparasites of an introduced warthog population. Since warthogs are a popular game species for recreational and 'biltong' hunting, and extensively hunted for damage reprisal, the study aimed to determine their potential for commercial game meat production as a sustainable management strategy. The meat from wild animals has often been sold under collective terms of 'game meat' and/or 'venison' but it has been suggested that wild animal muscles are sold separately rather than as the typical commercial cuts. The study therefore aims to investigate the effect of sex and age on the meat quality characteristics of six different skeletal muscles. In addition, there have been reports that the fresh meat from warthogs sometimes exhibits a flavour that is compared to boar taint, which is an undesirable odour and flavour that may occur in the meat from entire male domestic pigs (*Sus scrofa*), but has been associated with warthog meat from both genders and animals of different age classes. In order to elucidate on this, the study aims to determine the sensory profile of warthog meat (*Longissimus lumborum*) as influenced by sex and age. Furthermore, the use of meat in processed products could extend the value chain of game meat production and the study aims to develop and investigate the use of warthog meat in processed products. In totality, the study aims to encourage warthog meat utilization and consumption as a management strategy of introduced warthogs in South Africa.

References

Barnes, J. I., & de Jager, J. V. (1996). Economic and financial incentives for wildlife incentives on private land in Namibia and the implications for policy. *South African Journal of Wildlife Research*, *26*, 1–24.

Caro, T. M. (2005). Behavioural indicators of exploitation. *Ethology Ecology & Evolution*, *17*, 189–194. doi:10.1080/08927014.2005.9522608

Castley, J. G., Boshoff, A. F., & Kerley, G. I. H. (2001). Compromising South Africa's natural biodiversity - inappropriate herbivore introductions. *South African Journal of Science*, *97*, 344–348.

Crawford, M. A, Gale, M. M., & Woodford, M. H. (1970). Muscle and adipose tissue lipids of warthog, *Phacochoerus aethiopicus*. *International Journal of Biochemistry*, *1*, 654–658. doi:10.1016/0020-711x(70)90039-x

Hoffman, L. C. (2008). The yield and nutritional value of meat from African ungulates , camelidae, rodents, ratites and reptiles. *Meat Science*, *80*, 94–100. doi:10.1016/j.meatsci.2008.05.018

Hoffman, L. C., & Sales, J. (2007). Physical and chemical quality characteristics of warthog meat. *Livestock Research for Rural Development*, *19*, Article 153. Retrieved from http://www.lrrd.org/lrrd19/10/hoff19153.htm

Hoffman, L. C., Muller, M., Schutte, D. W., Calitz, F. J., & Crafford, K. (2005). Consumer expectations , perceptions and purchasing of South African game meat. *South African Journal of Wildlife Research*, *35*, 33–42.

Kiley-Worthington, M. (2014). Ecological agriculture. Integrating low input, high productive farming with wildlife conservation. Results from the experimental farm La Combe , Drome France. *Open Journal of Ecology*, *4*, 744–763.

Nyafu, K. (2009). *Warthog as an introduced species in the Eastern Cape*. MSc thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

Parkes, J., & Murphy, E. (2003). Management of introduced mammals in New Zealand. *New Zealand Journal of Zoology*, *30*, 335–359 Retrieved from http://www.tandfonline.com/doi/abs/10.1080/03014223.2003.9518346

Penrith, M.-L. (2009). African swine fever. *The Onderstepoort Journal of Veterinary Research*, *76*, 91–95.

Penzhorn, B. L. (1971). A summary of the reintroduction of ungulates into South African National Parks (to 31 December 1970). *Koedoe*, *14*, 145–159.

Poshiwa, X., Groeneveld, R. A., Heitkönig, I. M. A., & Prins, H. H. T. (2013). Reducing rural households ' annual income fluctuations due to rainfall variation through diversification of wildlife use : portfolio theory in a case study of south eastern Zimbabwe. *Tropical Conservation Science*, *6*, 201–220.

Somers, M. J. (1992). *The implications of social structure for the conservation and control of a warthog Phacochoerus aethiopicus population in the Andries Vosloo Kudu Reserve, Eastern Cape Province*. MSc Thesis, University of Pretoria, Pretoria, South Africa.

Spear, D., & Chown, S. L. (2009). The extent and impacts of ungulate translocations : South Africa in a global context. *Biological Conservation*, *142*, 353–363. doi:10.1016/j.biocon.2008.10.031

Van der Merwe, P., & Saayman, M. (2003). Determining the economic value of game farm tourism. *Koedoe*, *46*, 103–112. doi:10.4102/koedoe.v46i2.59

Van Schalkwyk, D. L., McMillin, K. W., Witthuhn, R. C., & Hoffman, L. C. (2010). The contribution of wildlife to sustainable natural resource utilization in Namibia: A review. *Sustainability*, *2*, 3479–3499. doi:10.3390/su2113479

Stellenbosch University http://scholar.sun.ac.za

Warren, R. (2011). *A Spending Model for Biltong Hunters*. MSc thesis, North West University, Potchefstroom, South Africa.

Wilfred, P. (2012). Trophy hunting and trophy size in Ugalla Game Reserve, western Tanzania. *Tanzania Journal of Science*, *38*, 111–122.

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Chapter 2
Literature Review

Abstract

Ungulate species are among the wildlife most often introduced globally for game farming, sport hunting, meat provision purposes, aesthetics or conservation. However, native wildlife may present a threat to both natural and modified habitats and incur environmental and economic costs. Common warthogs (*Phacochoerus africanus*) have been introduced to parts of South Africa that are considered to be the former range of the extinct Cape warthog (*P. aethiopicus*), although the exact historical distribution range of the two warthog species in South Africa remains relatively unknown. The common warthog has been classified as an invasive in parts of the country considering its associated impacts on the ecological and agricultural environment. However, the species may also be simultaneously considered as a pest and valuable game animal by stakeholders. This review attempts to provide a synopsis of the current biological and ecological knowledge on the common warthog relating to its historic and known distribution range in South Africa, its successful establishment and dispersal after introduction to central South Africa and the potential ecological and agricultural impacts associated with the species. The management of feral pigs (*Sus scrofa*) as an introduced species, and the utilization of the meat from wildlife animals are also discussed with regards to their implication towards warthog control and management.

1 Introduction

Large, terrestrial mammals have typically been introduced outside their range for game farming, sport hunting, meat provision purposes, aesthetics or conservation (Clout & Russel, 2007, Chown, Spear, Lee, & Shaw, 2009). Ungulate species are among the wildlife most often introduced for these purposes (Spear & Chown, 2009a). However, intentionally introduced ungulate species can become naturalized and able to disperse within the surrounding area (Fraser, Cone, & Whitford, 2000, Forsyth & Duncan, 2001). Non-native wildlife may present a threat to both natural and modified habitats and incur environmental and economic costs which lead to increased human wildlife conflict situations (Lowney, Schoenfeld, Haglan, & Witmer, 2005, Pimentel et al., 2001). The most important impacts associated with introduced ungulates are summarized in Table 1. Agricultural producers are regularly in conflict with wildlife that they perceive to threaten their livelihoods (Madden, 2004, Swanepoel, Leslie, & Hoffman, 2016., Chapter 4), and may respond by protecting crops or vulnerable livestock through killing and trapping problem species or transforming habitat (Treves, Wallace, Naughton-Treves, & Morales, 2006). However, since farmers recognize that wildlife has a social and economic value, they may simultaneously promote wildlife populations on their farm whilst trying to mitigate the damages caused (Conover, 1998).

The economic benefits derived from introduced ungulates often undermine their potential invasive threats (Castley, Boshoff, & Kerley, 2001). Ungulates are counted among the world's most invasive species viz feral pig (*Sus scrofa*), feral goat (*Capra hircus*) and red deer (*Cervus elaphus*) (Lowe, Browne, Boudjelas, & De Poorter, 2000). For example, feral pigs have been introduced onto every continent (except Antarctica) and after experiencing massive reproductive explosions, they reverted to the original wild appearance of their ancestors (Perez, 2005) and became serious ecological and agricultural pests. Feral pigs have the highest reproductive rate of all ungulates, achieved through high ovulation and pregnancy rates among adult and juvenile sows, the early onset of puberty in piglets, large litter sizes and short gestation periods. As agricultural pests, they raid crops (Schley, Dufrêne, Krier, & Frantz, 2008), kill and feed on young and eggs of certain animals (Choquenot, Lukins, & Curran, 1997, Elsey, Mouton, & Kinler, 2012, Carpio, Guerrero-Casado, Tortosa, & Vicente, 2014), are vectors of important animal and human diseases (Meng, Lindsay, & Sriranganathan, 2009) and are aggressive towards humans (Mayer, 2013). They are heavily persecuted for damage reprisal and also as a popular game animal for sport hunting and meat production (Bengsen, Gentle, Mitchell, Pearson, & Saunders, 2014, Gentle, Speed, & Pople, 2014).

Initially a species introduced outside of its natural distribution is referred to as an alien species, but if the alien species is able to survive in the new habitat, become established and spread through non-facilitated reproduction, it is referred to as an invasive species (Kolar & Lodge, 2001). For an introduced species to become an invasive species it needs to have a certain set of characteristics and undergo a number of transitional stages, with the time taken between different transitional phases depending on species traits and environmental factors (Kolar & Lodge, 2001). According to the literature, mammal species are more likely to become successful at establishing and spreading (Jeschke & Strayer, 2005, Jeschke, 2008) and becoming invasive (Clout & Russell, 2007) compared to other introduced organisms. A priority for invasion biology has been to identify the general drivers of the mammals' propensity towards invasion success, noting the significance of propagule pressure, biological and ecological suitability, and species characteristics and life-history traits (Forsyth, Duncan, Bomford, & Moore, 2004). Forsyth and Duncan (2001) found a significant relationship between invasion success and the number of individuals introduced for ungulates, while Forsyth et al. (2004) proposed that species have a greater chance of establishment when matched climatically to their new environment. Kolar and Lodge (2001) found the place of origin of the species to be a fairly good predictor of potential establishment, relative to its place of introduction. Colautti, Ricciardi, Grigorovich, and MacIsaac (2004) propose that all non-native species experience a reduction of enemies in introduced habitats due to biogeographic or anthropogenic barriers.

For mammals, Forsyth et al. (2004) associated invasion success with carnivores and omnivores rather than herbivores, species with smaller body sizes, a shorter maximum lifespan, larger litters and more offspring per year. Feral pigs are able to accelerate their life-history if there is a marked increased mortality among individuals of reproductive age (Hanson et al., 2009). Servanty et al. (2011) showed that compared to similar sized ungulates with an average life-history of six years, feral pigs in a lightly hunted population had an average generation time of 3.6 years, which was reduced to 2.3 in heavily hunted populations. This was achieved by sows timing the onset of oestrus according to climatic conditions and resource availability, and the contribution from juvenile sows participating in breeding events when they reach a threshold body weight of 27–33kg (33–41% of adult body mass). Gamelon, Besnard, and Gaillard (2011) also found that heavy hunting selects for earlier birth dates for piglets, which allows them to reach the threshold weight earlier and participate in breeding. According to Yessoufou, Gere, Daru, and Van der Bank (2014), evolutionary history is more important than life history traits to predict the invasive success of a mammal species. In other words, the higher a species evolutionary distinctness the more intensively an introduced mammal is able to invade. Detection and management of potential mammal invaders may therefore benefit from investigating their evolutionary past in addition to the species' life-history traits.

1.1 Ungulate introduction in South Africa

Prior to the nineteenth century and advancement of white settlers, the hunting of native wildlife for meat and animal products was an integral part of the indigenous San and Tswana communities (Morton

& Hitchcock, 2014), although the meat did not constitute a significant part to the Tswana diet. White settlers introduced horses, guns and ivory trading to the traditional hunting culture which largely replaced the hunting culture of the northern Tswana with trading and commercial farming incentives, whilst the western San communities and the white settlers continued to hunt wildlife. However, the change in wildlife hunting and utilization led to severe depletion of game animal populations (Bryden, 1893), which was further exasperated by colonial enforcement of land distribution and management in parts of southern Africa, and the destruction of natural habitat for agriculture. Large-scale ungulate species translocations were conducted in 1970's on several provincial and national reserves in South Africa in an attempt to re-introduce species that were thought to have gone locally extinct (Penzhorn, 1971). Conservation authorities allowed the introduction of mammals outside their natural range if the area of introduction was sufficiently fenced to enclose populations.

Exotic and native ungulate species valued as game animals are regularly introduced and/or translocated in South Africa for the game farming industry. The game farming industry relies on the utilization of wildlife through eco-tourism, recreational hunting, live game sales and meat production for personal or commercial gain (Van der Merwe & Saayman, 2003). The establishment and success of the industry in South Africa is attributed to the change in wildlife protection policies and private land-ownership during the 1960's and 70's, which encouraged wildlife protection and utilization on state-owned and private reserves (Benson, 1991). Thereby South African law permits landowners full ownership of all the animals that are contained within their property through adequate fencing, making both livestock and wildlife a valuable and tradable commodity. The modern game ranching industry is largely influenced by the demand of tourists and hunters for certain species and a great diversity of species, which is associated with increased economic activity even though most farms are naturally rich in wildlife biodiversity (Barnes & de Jager, 1996, Castley et al., 2001, Higginbottom & King, 2006). As a result, South Africa has the second highest rate of ungulate introductions globally, preceded only by the United States (Spear & Chown, 2009a). Castley et al. (2001) estimated that on average a game farm has 20 naturally occurring mammal species, while Dry (2012) stated that game farms currently play host to 45 mammal species on average, more than twice the natural estimate.

Extra-regional and extra-limital (intentional) introductions to farms around the country contribute to the homogenization of South African ungulate species compositions, and escapees (unintentional introductions) often form established naturalized populations (Clout & Russel, 2007, Spear & Chown, 2009b). This creates a type of artificial biodiversity that focuses on the economic value of species rather than their historical distribution and integration with the natural eco-system (Barnes & De Jager, 1996, Smith & Wilson, 2002), while McKinney (2005) concluded that extra-limital species are responsible for more biotic homogenization compared to extra-regional species. In South Africa, the practice appears to have been facilitated by the country's natural species richness and the lack of a national framework which governs the game farming industry (Spear & Chown, 2009a, Cousins, Sadler, & Evans, 2010). The latter has recently been recognized by the Department of Environmental Affairs who is in the process of developing a national framework for the norms and standards of translocation of indigenous species (Department of Environmental Affairs [DEA], 2015).

Table 1: The impacts associated with introduced ungulates on the natural and agricultural environment.

Associated impact	Reference
Natural environment	
Hybridization with native species	Biedrzycka et al., 2012
Resource competition	Focardi et al., 2000
Host foreign pathogens or parasites	Kelly et al., 2015
Degradation of vegetation units	Ali & Pelkey, 2013
Degradation of soil systems	Cuevas et al., 2012
Facilitation of further invasions	Holmgren, 2002
Homogenization of ecosystems	Spear & Chown, 2009b
Agricultural environment	
Crop damage	Herrero et al., 2006
Human casualties and vehicle accidents	Mayer, 2013, Mkanda & Chansa, 2011
Predation of animals and eggs	Choquenot et al., 1997, Schaefer, 2004
Infrastructural damage	Frederick, 1998

1.2 Warthog introductions

The common warthog (*P. africanus*) was introduced to various game farms and reserves in the Eastern Cape, Northern Cape and the Free State provinces of South Africa since the 1970's (Penzhorn, 1971). The first introductions by conservation authorities were considered a re-introduction of the warthog species (*P. aethiopicus*) believed to have gone locally extinct. Further introductions onto private game farms-and-reserves followed as the species are considered charismatic and contribute to tourist and hunter satisfaction (Maciejewski & Kerley, 2014). According to Penzhorn (1971) an unknown number of common warthogs, sourced from the Hluhluwe-IMfolozi Park (KwaZulu Natal), were introduced onto the Golden Gates Highlands National Park (GGHNP), Free State province, between 1963 and 1968. Another group of warthogs (N=20) also sourced from Hluhluwe-IMfolozi were introduced onto the Andries Vosloo Kudu Reserve (AVKR) (which now forms part of the Great Fish River Nature Reserve) in the Eastern Cape province between 1976 and 1977 (Somers, 1992). In 1984, three warthogs were translocated from the Andries Vosloo Kudu Reserve to the Rolfontein Nature Reserve (RNR) in the Northern Cape province (Unpublished reserve records). The recorded introduction events were reported to have been successful, with warthog populations becoming established and increasing through non-facilitated reproduction. According to official reserve records the warthog population in RNR ranged around 300 in 2008, which forced the parks' management to introduce control efforts. From 1991 onwards, a certain number of warthogs were shot or caught and translocated to other reserves within the Northern Cape province annually. Despite these control measures, warthogs remained numerous and abundant within the reserve.

While larger mammals are typically contained using wire fences or wire netting, warthogs have a habit of undermining fences by digging holes underneath, or breaking though wires and wire netting. This allowed them to escape enclosures and become free-roaming, establishing naturalized populations, reproduce and disperse in within the introduced habitat, and exert negative impacts on the natural and agricultural environment. In addition, common warthogs have been observed to transverse sizable river bodies in the Limpopo and Northern Cape provinces, although this has not been noted in published literature. Current regulation of activities pertaining to native and extra-limital warthogs is determined by individual provincial authorities. The major activities and regulations are summarized in Table 2. However, in terms of the National Environmental Management: Biodiversity Act (10/2004): Norms and Standards for the translocation of indigenous species in South Africa (DEA, 2015), warthogs are listed among the species to which an application for exemption of permits in terms of provincial legislation may be considered. Nyafu (2009) determined that introduced warthogs are regarded as a high risk species to the ecosystem and the agricultural sector by agricultural producers and landowners of the Eastern Cape province, and has subsequently classified the species as an invasive in the region. They are considered an agricultural pest in their natural range and cause damage to fences, crops and pastures, natural grazing fields, roads and other infrastructure (Mason, 1982, Somers, 1992, Vercammen & Mason, 1993, Treydte, Bernasconi, Kreuzer, & Edwards, 2006). To date, no study has attempted to quantify the actual extent of the damage they cause either ecologically or economically in the introduced range. It has been postulated that they could severely impact upon vegetation since they are hyper-grazers with destructive feeding habits (Mgqatsa, 2010, Smit, 2014).

Table 2: The regulations of activities pertaining to warthogs as determined by provincial authorities.

Province	Hunt/catch/kill	Importing/exporting/ translocating	Possessing/ controlling	Trading/buying/ selling
Limpopo	Require permit	Require permit	Require permit	Permit not required
North West	Require permit	Prohibited	Prohibited	Prohibited
Eastern Cape	Permit not required	Require permit	Permit not required	Permit not required
Northern Cape	Require permit	Prohibited	Prohibited	Prohibited
KwaZulu Natal	Require permit	Require permit	Permit not required	Require permit
Mpumalanga	Permit not required*	Require permit	Require permit	Require permit[#]

Free State	Permit not required**	Require permit	Permit not required	Require permit
Gauteng	Require permit	Require permit	Require permit	Require permit
Western Cape	Require permit	Prohibited	Prohibited	Prohibited

*Permission from landowner.
**If registered as game animal trader.
#If game animal is alive, written consent if game animal is a product.

1.3 History of two warthog species

Two species of warthog occur on the African continent, the genetically divergent common warthog (*P. africanus*) and the Cape (or desert) warthog (*P. aethiopicus*) (Randi, D'Huart, Lucchini, & Aman, 2002). Its common ancestor diverged about 4.5 million years ago during the second part of the Pliocene when extreme climatic conditions isolated populations to very arid habitats which, together with the inability of warthogs to disperse over long distances, resulted in the evolution of two distinct species of warthog occupying different parts of Africa, and the disjunct distribution of the Cape warthog in Africa (Muwanika, Nyakaana, Siegismund, & Arctander, 2003, Grubb & D'Huart, 2010). According to Coe and Skinner (1993), during the extended periods of extreme arid conditions of the Pliocene the majority of South Africa was covered by the Kalahari sands which had a profound effect on the distribution and evolution of mammalian fauna. The distribution of the Cape warthog is shared by 10% of southern African sub-region mammal species, including the black backed jackal (*Canis mesomelas*), bat eared fox (*Otocyon megalotis*), aardwolf (*Proteles cristata*), mountain reedbuck (*Redunca fulvorufula*), white rhinoceros (*Ceratotherium simum*) and Kirk's dikdik (*Madoqua kirkii*) (Grubb, Sandrock, Kullmer, Kaiser & Schrenk, 1999). All these species are absent from the extensive Brachystegia-Mopane woodlands of central Africa and their distribution is ascribed to habitat specialization in the Guinea and Sudan savannas and grasslands.

The common warthog is considered to be a habitat generalist, inhabiting a wide range of moist and dry African savannah grasslands, open bushlands and woodlands, with varied climatic conditions across the continent (Cumming, 2008). Its range extends from the sub-Saharan parts of the continent, from Senegal in the west to Ethiopia in the east, through central Africa to southern Africa, including Zimbabwe, South Africa and Swaziland, while being locally absent in some parts (Skinner & Chimimba, 2005). They are not found in the extreme northern parts of Africa including Algeria, Libya and Egypt, as well as central Africa including large areas of the Democratic Republic of the Congo and Angola. In South Africa, their known natural range includes the upper north-eastern parts of the country including the Limpopo, Mpumalanga and marginal parts of the KwaZulu Natal/Mozambique border (Rautenbach, 1982, Skinner & Chimimba, 2005, Skead, Boshoff, Kerley, & Lloyd, 2007). Inland, warthogs also occur in the northern parts of North West province and the border of the Northern Cape and Botswana. They occurred historically in Lesotho (Boshoff & Kerley, 2013) and likely currently occur at low densities along the Caledon River in Lesotho (Swanepoel, Schulze, & Cumming, in press.).

The extinct Cape warthog occurred as a geographically isolated population in South Africa and possibly Namibia. The first specimen was collected from the colonial Cape province and sent to present-day Netherlands, where it was described and named in 1766 (Ellerman, Morrison-Scott, & Hayman, 1953). The first common warthog specimen was also described in the same year, from skeletal remains found in present-day Senegal, while the first specimen from South Africa was collected by Wahlberg from present-day KwaZulu Natal in 1846 (Sundevall, 1846 in Grubb & D'Huart, 2010). Interestingly, the Oxford University Museum of Natural History recently discovered a common warthog skull in their Tradescant Collection acquired sometime between 1656 and 1678, making it the oldest specimen in Europe, predating the aforementioned specimen by at least 100 years (D'Huart, Nowak-Kemp, & Butynski, 2013). Palaeontologists originally recognized the occurrence of two warthog species on the African continent based on remains from the Holocene and Pliocene period, but this distinction became obscured sometime during the 20th century when numerous authors came to regard warthogs as belonging to one polytypic line, designated as *P. aethiopicus*. This is discussed in detail by Grubb and D'Huart (2010) in their review on the occurrence and identification of the Cape and common warthog during the 19th and 20th century. The authors postulated that the reason for the misclassification was that as the Cape warthog became extinct, increasingly more *P. africanus* material from across Africa became available, and there was a lack of *P. aethiopicus* specimens available for examination and comparison. Owen (1845 in Grubb & D'Huart, 2010) stated that the warthogs from South Africa shed their incisors at an advanced age, while the warthogs from northern territories (outside of South Africa) retained their incisors throughout life. Lönnberg (1908) studied warthog skulls from the British museum and recognised five species, but Shaw (1939) concluded that skull proportions cannot be used to identify species as there is considerable variation within a single species. As the differentiation of warthog species were not known to all scholars during the 20th century, it was generally accepted that northern populations of *P. africanus* were the same species that had gone extinct in South Africa.

The local extinction of *P. aethiopicus* species was largely attributed to the rinderpest epidemic that raged through Africa from 1886 to 1897, responsible for massive livestock and wildlife losses. However, since the last *P. aethiopicus* specimen was collected in 1871, it has been suggested that the advancement of white settlers and bulk-grazing domestic livestock decimated populations and transformed viable habitat, as *P. aethiopicus* are considered specialized grazers (Nyafu, 2009). This is supported by the high degree of hypsodonty and delayed root formation of the species which reduces rate of tooth wear; an evolutionary adaption to grazing of C4 plants with high accumulated levels of silica (Mendoza & Palmqvist, 2008, Hummel et al., 2011). Whether indigenous peoples contributed to the hunting pressure on *P. aethiopicus* populations remains debateable as some accounts maintain that indigenous peoples such as the San never hunted warthogs for meat, at least not with spears (Sclater, 1900), although skeletal remains of warthog species have been found in bushman caves (Hewitt in Shortridge, 1934). The introduction of firearms with white settlers notably reduced the abundance of wildlife populations and altered their distribution in southern Africa, according to Bryden (1893). Together with increased hunting pressure and habitat loss, it is possible that the rinderpest epidemic killed off the last of the increasingly isolated populations which led to local extinction.

The discovery of *P. aethiopicus* populations in eastern Africa, based on morphological analyses, prompted a review of warthog systematics in the 21st century to again formally acknowledge the existence of two different monophyletic lineages, which DNA sequencing subsequently proved (Grubb & Oliver 1991, Randi et al. 2002). The common warthog was reverted back to its correct name, *P. africanus*, with the Cape warthog populations represented as *P. aethiopicus sundevalli,* and the desert warthog as *P. aethiopicus delamerei*. The desert warthog occurs in parts of Kenya, Somalia and Ethiopia, along with the common warthog (D'Huart & Grubb, 2001, De Jong, Culverwell, & Butynski, 2009, Obanda et al., 2011). The two species may co-occur in certain parts of their distribution range but there is no information on how they partition for resources and habitat, interact with one another or whether hybridization is possible. However, the latter is considered unlikely due to the high genetic divergence between the species.

The exact historical distribution ranges of the two warthog species in South Africa remains relatively unknown as there is paucity in the records of warthog occurrence in central and northern parts of South Africa. It is interesting that the occurrence of warthogs, one of the most easily distinguishable pigs based on their facial wart-like protrusions, was not referenced more accurately by European explorers (Skead et al., 2007). However, Bryden (1893) noted it curious that the warthog was not seen more often than not on his extensive travels through central South Africa. According to Boshoff and Kerley (2013) and Boshoff, Landman, and Kerley (2015), historical accounts imply that *P. aethiopicus* did not occur north of the Orange river in South Africa or that *P. africanus* occur south of the river, suggesting the river acts as a biogeographical boundary. During his travels across central South Africa, Burchell (1822, 1823) also suggested the Great River (Orange River) represents a biozoological boundary in the land. As mentioned, common warthogs have been observed to transverse sizable river bodies in the Limpopo and Northern Cape provinces, although this has not been noted in published literature. Although there is no conclusive evidence regarding the exact historical distribution of the two warthog species in South Africa, it is suggested that *P. aethiopicus* was possibly the true South African warthog species which was historically widely distributed across South Africa and Namibia according to fossil evidence and their ability to survive under more extreme climatic and environmental conditions associated with the Cape, Karoo and Namibia (Roberts, 1951, Kingdon, 1997).

The vegetation map of South Africa provides support for the demarcated distribution ranges of the two species (Figure 1), a consideration suggested when reviewing the known historical distribution of terrestrial mammals (Boshoff & Kerley, 2001). The Cape warthog is considered a specialist grazer, and was therefore likely adapted to utilize grassland vegetation, while the common warthog is also a grazer but may include large proportions of browsing material in its diet as available (Skinner & Chimimba, 2005, Nyafu, 2009). The distribution of the common warthog appears to have been more restricted to northern parts of the country where they could exploit both grazing and browsing material from the savanna bushveld vegetation.

Fossil remains indicate that *P. aethiopicus* occurred north of the Orange River to a wider and more abundant extent than *P. africanus*, but became increasingly restricted to their southward distribution range (Ewer, 1957, Skinner & Chimimba, 2005). *P. aethiopicus* fossil remains have been found as far north as the Kalkbank Middle Stone Age site in northern Limpopo (Ewer, 1957) and live specimens and a skull obtained from KwaZulu Natal were described as *P. aethiopicus* (Sclater, 1871, 1891, in Grubb & D'Huart, 2010). Confirmed sightings of live Cape warthogs, and later identification of their skulls, were made near Port Elizabeth and Zuurberg hills, and near the Sondags River in the Eastern Cape province (Lönnberg, 1909 in Grubb & D'Huart, 2010). A *P. aethiopicus* skull was obtained by Burchell in 1813 near the Orange River in the vicinity of Hopetown, but unfortunately the exact locality is uncertain. Of the warthog skulls in South African museums, two were obtained from the eastern Transvaal (present day Mpumalanga province, Figure 2) and confirmed as *P. africanus*, and one from Damaraland in northern Namibia confirmed as *P. aethiopicus* (Sclater, 1900, Ewer, 1957).

Thackeray (1979) found warthog bone fragments pertaining to the Late Stone Age in archaeological caves in southern Namibia and considered the remains to be an indication of the local faunal community of that time period. Klein (1988) found warthog remains probably pertaining to the Middle Stone Age period in archaeological sites at Wonderwerk caves near Danïelskuil, Kathu caves near Posmastburg and the Power's cave near Kimberley, adjacent to the Vaal River. It was not determined in both studies whether these were *P. aethiopicus* or *P. africanus.* Fossilised or semi-fossilised teeth that cannot be distinguished from *P. africanus* have been found in South African fossil deposits but these are generally rarer than for *P. aethiopicus*, while the typical molar fossils of *P. africanus* are not known from the Free State (Wells, Cooke, Malan, Wells, & Cooke, 1942, Cooke, 1949). Dreyer and Lyle (1931) identified three different species of warthogs (*P. venteri, P. meiringi* and *P. dreyeri*) from fossil deposits in the province, but other authors (Van Hoepen, 1932, Cooke 1949, Ewer, 1957) maintained that all three were synonyms for *P. aethiopicus*. Wells et al. (1942) found that the greater part of warthog fossil remains found at the Vlakkraal site belonged to *P. aethiopicus*, and the undoubted presence of the species overshadow the likelihood of *P. africanus* occurring there historically, as unidentified fossil teeth cannot be distinguished from *P. aethiopicus*. Dreyer and Lyle (1931) and Van Hoepen and Van Hoepen (1932), acknowledged the occurrence of another warthog species, *P. helmei*, distinct from *P. africanus* in this region, which was proposed by Ewer (1957) to be a subspecies of *P. africanus* (*P. africanus helmei*), geographically isolated to the Free State province, but factors responsible for its restriction, and extinction, remain unknown. The warthog fossils found in the Bundu Farm Pan site, 70 km west of Prieska, could not be distinguished to species level (Kiberd, 2006). Most of the remains are considered to represent the paleoecology faunal distribution during the Middle Stone Age from animal predation and not human hunting.

Rautenbach (1982) found no written records or specimens of *P. africanus* from the southern Transvaal (Figure 2) or northern Free State, with the most southward records limited to Rustenberg, Pretoria and Zeerust. Sclater (1900) reported that warthogs (designated as *P. aethiopicus*), were not uncommon in the areas of Lydenburg, western Transvaal (North West province), in Mashonaland (northern Zimbabwe) and Damaraland. Shortridge (1934) documented the occurrence of warthogs in Southern West Africa, present-day Namibia. According to accounts from native peoples, warthogs occurred across Namibia and were abundant in northern Koakoland, and rare in the coastal areas of Zestfontein and westwards towards the Maltahöhe district, but were not known from the Orange or Fish River according to the author. Interviews with old residents of Louisville and Upington (northern North Cape) revealed that while there was a warthog species believed to be *P. aethiopicus* historically present, it went extinct during the latter part of the 19th century (Shortridge, 1934, 1942). They were also considered as extinct in the area south of Great Namaqualand (central Namibia) in the west and through to the south of Zululand by that time. Interestingly, no historical accounts indicate as to whether *P. africanus* experienced similar population extirpation in its southern African range, as the species appear to have persisted in its northern habitat. In order to elucidate on the success of common warthogs as an introduced species, the introduction events and associated biogeographical conditions are discussed in this review here.

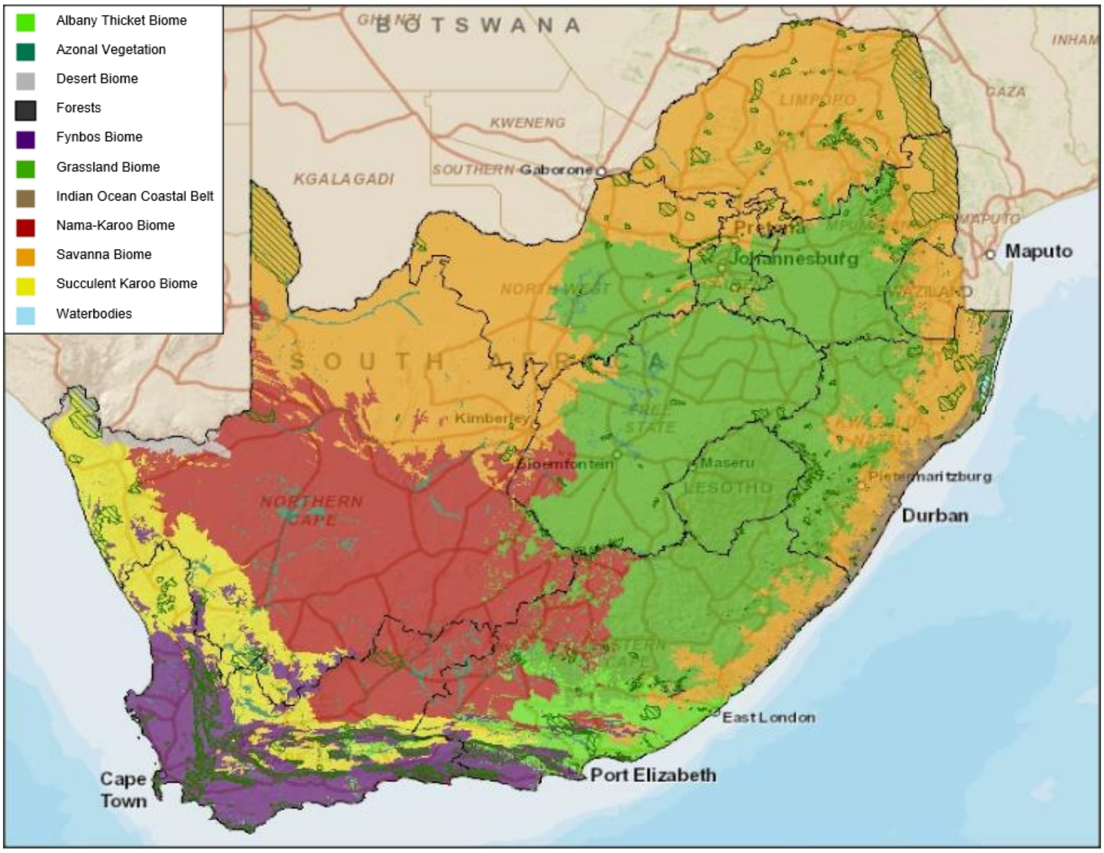

Figure 1: The vegetation biomes of South Africa (Source www.sanbi.org).

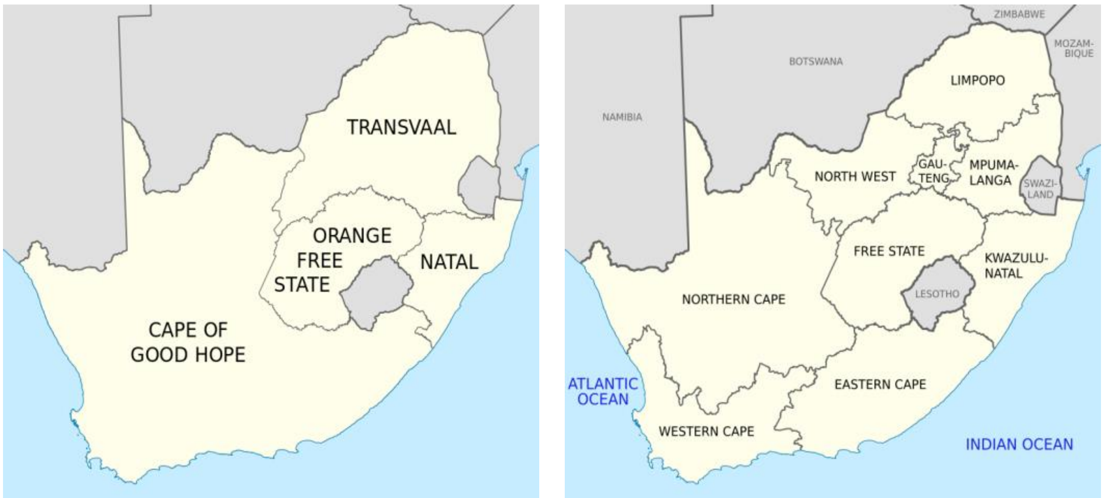

Figure 1: The former (<1994) and current (>1994) provinces of South Africa (Source: https://commons.wikimedia.org. Licensed under CC BY-SA 3.0 via Commons).

1.4 Warthogs as an introduced species

Warthogs have been introduced to areas where the main vegetation types are primarily grassland, thicket and Nama Karoo, and it is expected that their dispersal and range expansion will continue due to their dietary flexibility and the geographical expansion of farming enterprises. The National Red List Assessment has recently updated the distribution map for this species to include the distribution of introduced populations in South Africa, making use of warthog distribution records collected by Swanepoel during post graduate research which has been published in part in Swanepoel, Schulze, and Cumming (in press.) (Figure 3). The mapping methodology is provided in The Red List of Mammals of South Africa, Swaziland and Lesotho (Child, Raimondo, Do Linh San, Roxburgh & Davies-Mostert, in press.). The map illustrates the expansion of the common warthogs' distribution range in South Africa including the historic distribution records.

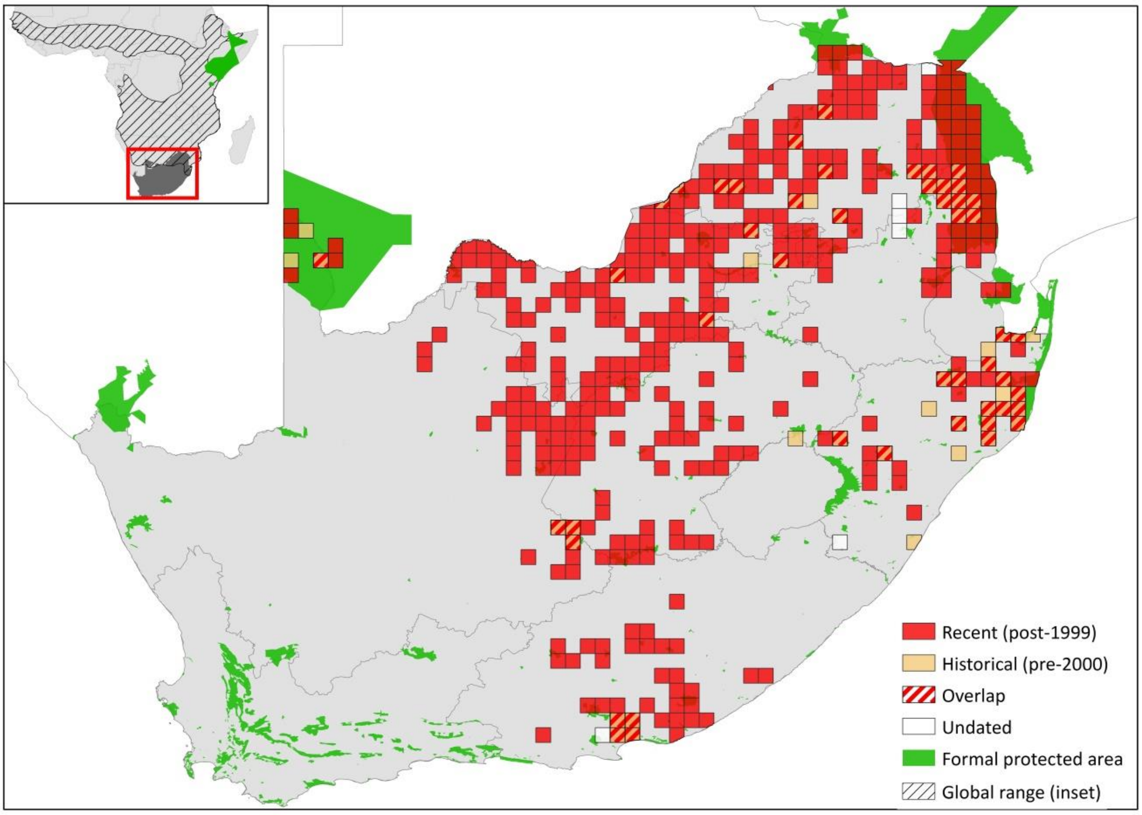

Figure 2: Distribution records for common warthog (*Phacochoerus africanus*) within the assessment region (Source: Swanepoel, Schulze, & Cumming, in press.).

In addition to natural grazing, the prevalence of agricultural activities in areas where crops, fodder and pastures are cultivated commercially might provide year-round food for warthogs. All three provinces of introductions viz Eastern Cape, Northern Cape and Free State provinces are important agricultural producers utilizing the majority of land for farming purposes, and Bamford, Ferrol-Schulte, and Wathan (2014) found warthog presence were positively influenced by the occurrence of pastoral farms. The Northern Cape covers an area of 363 389 km^2 of which 81% is utilized for agricultural purposes. The major agricultural activity is stock farming, including cattle (*Bos taurus*), sheep (*Ovis aries*), and goat (*C. hircus*). Crop farming only comprises 2% of the total land use as the area is arid. The Free State province covers 129 825 km^2 with agriculture accounting for 90% of the land use, of which about 57% is used for livestock farming and 33% for crop production. The Eastern Cape covers 170 616 km^2 of which 86% is used for farming (Department of Agriculture, Forestry and Fisheries [DAFF], 2013a). Game farming has also become a major form of agricultural land-use, with game farms covering 48 520 km^2 (13.4% of total area) of the Northern Cape and 1 477 km^2 (1.14% of total area) of the Free State and provinces. Game farms covered a total of 3 728 km^2 (2.2% of total area) in the Eastern Cape in 2002 (Smith & Wilson, 2002).

Livestock and game farms also offer permanent water sources in the form of artificial dams and troughs. The common warthog is usually within range of perennial surface water but appears to be the least water-dependent member of the Suidae family (Harris & Cerling, 2002). Smit (2014) postulated that their preference for areas with perennial surface water is due to the association of these marshy areas with grazing lawns of *Cynodon dactylon*. Other than access to food and permanent water sources, introduced warthogs also had access to burrows as other species involved in digging burrows (aardvark [*Orycteropus afer*] and porcupine [*Hystrix africaeaustralis*]) are widely distributed across South Africa. Burrows are used to raise piglets during the farrowing season, for thermoregulation and as refuge against predators (Sowls & Phelps, 1966).

Warthogs are non-territorial and non-migratory animals with large distribution ranges in their native habitat (Somers, Penzhorn, & Rasa, 1994). Their home ranges may stretch across a number of fenced properties which may include crop, livestock and game farms, and private or public nature reserves, which defines them a free-roaming species. The conservative estimated number of common warthogs in southern Africa (Angola, Zambia, Tanzania and southwards) is about 250,000 (Cumming, 1999), but is estimated to be higher due to the increasing availability of suitable habitat for warthogs from the expansion of game ranches across the country. Typical densities range between 1 and 10 per km^2 in protected areas (Hunter, 1998, Caro, 2005), but local densities of 77 per km^2 were found on short grass in Nakuru National Park (Radke, 1991 in Cumming, 2008). Estimated densities in Kruger National Park were 0.25 warthogs per km^2 (Ferreira et al., 2010), and ranged between 26.0 per km^2 in 2006 and 22.8 per km^2 in 2007 in the iMfolozi Game Reserve, KwaZulu Natal (White, 2010).

The species is highly fecund with high reproductive rates, have a polygynandrous mating system and exhibit little territorial behaviour as males actively compete for mating opportunities and not habitat. They typically reach sexual maturity around 18-24 months, but juvenile females less than 12 months of age have been found pregnant (Somers, Rasa, & Penzhorn, 1995). According to Clough (1969), they can reproduce aseasonally in high rainfall regions where resources are plentiful, but have distinct farrowing peaks in October and April in regions with a marked dry and wet season as found in central South Africa. Populations in the Andries Vosloo Kudu Reserve (AVKR) had an estimated annual growth of 45% (Somers & Penzhorn, 1992), 56% in RNR and 62% in Tussen-die-Riviere Nature reserve in the Free State province (Unpublished reserve data). The highest annual growth rates recorded on the latter reserve were 106%. Litter sizes vary between 1 and 5 piglets, while average litter sizes recorded are 3.7 (Child, Roth, & Kerr, 1968), 2.6 (Boshe, 1981), 3.3 (Mason, 1982) and 4 (Somers & Penzhorn, 1992). Adoption may occur when a closely related female of the sounder with young is lost to predation or disease and another lactating female will raise the young as her own. Piglet mortality is further reduced through facultative communal cooperative breeding where yearlings or closely related females can assist in raising young, with allo-suckling occurring in 55% of matriarchal sounders (Plesner-Jensen, Siefert, Okori, & Clutton-Brock, 1999, White & Cameron, 2009). Both sexes are considered strongly philopatric with sounders belonging to clans of related individuals within a population (Muwanika, Nyakaana, & Siegismund, 2006). Individuals that remain in their natal range may enjoy benefits such as access to high quality habitat, increased protection from predators or increased fitness (Begon, Townsend, & Harper, 2006).

Major predators of warthogs are lions (*Panthera leo*) and leopards (*Panthera pardus*), and others include spotted hyenas (*Crocuta crocuta*), cheetahs (*Acinonyx jubates*), African wild dogs (*Lycaon pictus*) and crocodile (*Crocodylus niloticus*) (Skinner & Chimimba, 2005). Somers and Penzhorn (1992) found predation to be a minor contributor to warthog mortality in the AVKR where leopards were the only predator present. The presence of lions (*P. leo*) and spotted hyenas (*C. crocuta*) did not affect warthog population growth in Addo Elephant National Park but did impact on population age structure (Mgqatsa, 2010), while the presence of lions, leopards and African wild dogs influenced the spatial distribution of warthogs in a private game reserve (Thaker et al., 2011). The geographic success of warthogs could therefore partially be explained by the Enemy Release Hypothesis, which states that the absence of native enemies aids exotic species in distributing and becoming abundant (Keane & Crawley, 2002). Matthee, Swanepoel, Van der Mescht, Leslie, and Hoffman (2013, Addendum A) investigated the ecto-parasites of introduced warthog populations in the Free State province and found low levels of ecto-parasite species richness in the introduced population compared to those of natural populations, providing support for the Enemy Release Hypothesis.

Humans can be considered as a major predator of warthogs as they are heavily hunted in their natural range for meat and ivory (tushes), and trophy hunting (Caro, 2005, Wilfred, 2012). In 2009 a total of 2049 warthogs were officially recorded as being hunted by international trophy hunters in South Africa which increased to 3 849 in 2013, making warthogs the 2nd most often trophy hunted in South Africa (Professional Hunters Association of South Africa [PHASA], 2014). These numbers however do not represent all the warthogs hunted in the country as it is expected that the majority of recreational and damage control hunting remain unreported. Introduced populations in the GGHNP, AVKR and RNR initially enjoyed protection from human induced mortalities, while populations introduced onto game farms may possibly have experienced a lag period after introduction during which the species progressed from initial introduction to establishment. The ability of a propagule to disperse across long distances correlates positively with the rate of spread of a non-native species into a habitat (Neubert & Caswell, 2000). Muwanika et al. (2003, 2006) maintained that the genetic structure of warthogs discourages natural re-colonization of locally extinct populations through dispersal, while indicating dispersal is male-biased but significantly limited by distance. Species could overcome the dispersal barrier by either being a) present as a source population to close proximity of the invaded habitat or b) introduced during multiple and frequent events in sufficient numbers e.g. propagule pressure. Initially warthog dispersal and spread would have been achieved through high propagule pressure and subsequently aided by already established source-populations. High propagule pressure increases genetic diversity and decreases chances of a genetic bottleneck. Additionally, hunting pressure may possibly contribute to warthog dispersal and spread, and alter behaviour patterns. For example, Shortridge (1934) reported that warthogs become increasingly nocturnal amidst heavy human persecution. Nyakaana, Abe, Arctander, and Siegismund (2001) and Muwanika et al. (2006) found a breakdown in social structure due to poaching of elephant (*Loxodonta africana*) and common warthog populations, respectively, which resulted in genetically amalgamated populations with reduced heterozygosity. A breakdown in social structure can negatively influence philopatric behaviour, leading to increased-distance dispersal events and subsequent range expansion.

In terms of the invasion process, warthogs have 1) escaped from their original introduction points, 2) dispersed and formed established, naturalized populations in the new habitat, 3) successfully started reproducing and dispersing over large distances to colonize other parts of the habitat, and 4) started exerting negative ecological and economic impacts on the environment. Being herbivores, and omnivores in the case of feral pigs, introduced ungulates may exert important impacts on the ecological and agricultural environment (Wardle, Barker, Yeates, Bonner, & Ghani, 2001, Spear & Chown, 2009b). The economic benefits derived from introduced ungulates therefore often undermine their potential invasive threats. This case can be compared to a certain extent with the introduction and invasion success of the feral pig, as Lowe et al. (2000) count feral pigs among the most invasive species in the world. The introduced common warthog is therefore part of a unique paradigm where a wildlife species can be considered, and subsequently managed, as either a damage-causing or valuable species. This conflicting approach to management may result in unethical and unsustainable control practices with undesirable outcomes for both farmers and warthogs. According to the International Union for Conservation of Nature Species Survival Commission (IUCN/SSC, 2013), the translocation of species should rather considered biological aspects that might be influenced, such as the availability of habitat, the potential negative impacts the species might exert, and the risk of hybridization and disease transmission. As noted by Bernard and Parker (2006) the most recent information on the distribution of a species in South Africa should be considered more important as reliable records of historical distribution is lacking.

2 Associated impacts

2.1 Natural environment

As herbivores and often omnivores, exotic ungulates can have significant impacts on the introduced habitat (Pimentel et al., 2001). They may directly impact upon the native vegetation which can lead to degradation, inhibition of recovery after disturbance or long-term alteration of structure and composition (Bond & Loffell, 2001, Raffaele, Veblen, Blackhall, & Tercero-Bucardo, 2011). Certain habitats are more susceptible to the impacts of introduced herbivores, viz ecosystems that have evolved without mammalian herbivores, or habitats where the introduced herbivores are functionally different from, or can obtain higher densities than, the native herbivores (Vazquez, 2002). For example, browsing by introduced giraffes (*Giraffa camelopardalis*) led to differential mortalities of *Acacia* species, causing extirpation of more sensitive species within the study area (Bond & Loffell, 2001), while removing native predators can exacerbate the effect of native or introduced herbivores as densities exceed ecological carrying capacities (Stockton, Allombert, Gaston, & Martin, 2005). Conversely, plant communities that have evolved with high levels of herbivory have increased tolerance and resistance to mediate the impact of increased herbivory on fitness (Bailey & Schweitzer, 2010). In these habitats, herbivores are considered ecosystem architects that maintain or alter vegetation integrity through resource regulation and positive feedback loops (Craig, 2010). Any change in herbivore pressure may have positive, negative or neutral effects on the vegetation unit, depending on the relevant spatial scale under observation (Fuhlendorf & Smeins, 1999).

Feeding guild, functional herbivory and dietary flexibility within a habitat are important factors to consider when evaluating the impact herbivores may have on floral and faunal communities. In their natural habitat, the common warthog is considered a selective grazer since they actively select the more nutritious parts of grasses containing high levels of nitrogen, phosphorous and crude protein (Cromsigt & Olff, 2006, Treydte et al, 2006). Their diet consists primarily of C4 grasses depending on availability;

to supplement they may include forbs, woody shrubs, fruits and succulents, agricultural crops, animal material and carrion. Some authors therefore refer to them as mixed feeders but growing scientific evidence suggests that herbivores can exhibit surprising levels of dietary flexibility according to spatio-temporal variations (Codron et al., 2007a, Codron & Codron, 2009). In north central Namibia, the diet of the indigenous Sanga cattle (*B. taurus africanus*), which are considered specialist grazers, consist of up to 84% C3 plant material in dense woodland habitats (Radloff, Van der Waal, & Bond, 2013). Marquez and Boecklen (2010) also found that introduced gemsbok (*Oryx gazella*) in New Mexico may include up to 44% C3 shrubs in their diet despite being primary grazers in their native range. Feral pigs exhibit dietary plasticity according to food availability, seasonal and geographical variation and energy requirements. Its (feral pig) diet consists mainly of plant material but increased intake of animal matter, live and from scavenging, has been observed among introduced populations (DeVault & Rhodes, 2002, Ballari & Barrios-García, 2014). In regions of crop production Herrero, García-Serrano, Couto, Ortuño, and García-González (2006) found that the diet of feral pigs consists of agricultural plants (88.74%), of which 77.08% was maize (*Zea mays*). In arid environments feral pigs are able to survive by maximising their dietary energy intake through selective foraging of foodstuffs rich in carbohydrates (Cuevas, Ojeda, Dacar, & Jaksic, 2013).

The proportion of C4 plants in warthog diet vary from 75-100% depending on region (Table 3), and they are able to increase the proportion of C3 plants in their diet without discernible negative impacts on their fitness. Literature has maintained that they tend to consume more roots and bulbs during winter (Mason, 1982), but no significant seasonal shifts have been observed in their grass intake, and they may include other material in their diet regardless of season, including forbs, woody shrubs, fruits and succulents (Treydte et al., 2006, Codron et al., 2007a, Nyafu, 2009). Unpublished data on the carbon isotope composition of an introduced warthog population in the Free State province found their diet consisted primarily of C4 plants across three seasons.

Warthogs are generally associated with burnt areas or areas showing various degrees of over-utilization, and are usually of the first mammals to inhabit previously disturbed habitats such as cattle paddocks and bomas, potentially promoting nutrient turnover in soils and grasses (Wentzel, Bothma, & Van Rooyen, 1991, Treydte et al., 2006, Treydte & Halsdorf, 2006). Warthogs are highly selective regarding their food intake in terms of nutritional content, with the nitrogen content of their faecal matter remaining stable across seasons as opposed to other bulkgrazers (Botha & Stock, 2005, Treydte et al., 2006). Smaller ungulates such as warthogs have increased metabolic rates and are dependent on high quality fodder to meet their nutritional requirements (Codron et al., 2007b). Field (1970) observed them targeting the tiller bases of perennial grasses where the bulk of carbohydrates are stored. Being a hindgut fermenter, they are able to digest fibre more efficiently. Clauss et al. (2008) found captive warthogs to achieve an apparent digestibility of neutral detergent fibre (NDF) of 63-66%, and acid detergent fibre (ADF) of 59-62%. According to Wentzel et al. (1991), warthogs prefer grass species of the Increaser II category as defined by Trollope (1989) which includes *Heteropogon contortus, Eragrostis* spp., *Shmiditia papophoroides, Aristida congesta, Chloris virgata* and *C. dactylon.* In the Hluhluwe iMfolozi Park, which forms part of their native range, they have been observed to include notable proportions of highly palatable *Panicum maximum* and *Themeda triandra* grasses in the dry season, but largely exclude *T. triandra* (a tall bunch grass) in the wet season (Kleynhans, Jolles, Bos, & Olff, 2011).

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Table 3: The percentage of C4 material common warthogs include in their diet according to distribution.

Country	Study area	Vegetation type*	C4 %	Reference
Native				
Tanzania	Saadani Game Reserve	Open savannah and coastal forest	98%	Treydte et al., 2006
Tanzania	Former cattle ranch	Cattle grounds on open savannah	77–98%	Treydte et al., 2006
Tanzania	Saadani Game Reserve	Humid savannah	100%	Harris & Cerling, 2002
Kenya	Various	Wooded and bushy grassland	100%	Harris & Cerling, 2002
Zaire	Garambi National Park	Grassland savannah	100%	Harris & Cerling, 2002
Uganda	Queen Elizabeth Park	Grassland savannah and humid forests	80-90%	Harris & Cerling, 2002
South Africa	Kruger National Park	Mopane and thorny bushveld	91%	Codron et al., 2007a
South Africa	KwaZulu Natal	Lowveld and thornveld	75%	Nyafu, 2009
Introduced				
South Africa	Eastern Cape	Valley and dune thicket	71%	Nyafu, 2009
South Africa	Free State	Grassland savanna	100%	Radloff, unpublished data

*As described by author(s).

Many studies maintain that the role of non-native herbivores as seed dispersers of exotic plant species is greatly underestimated (Constible, Sweitzer, Vuren, Schuyler, & Knapp, 2005, Calvino-Cancela, 2011, Davis, Forsyth, & Coulson, 2010). Introduced herbivores directly facilitate the dispersal of exotic plant seeds through endozoochory and epizoochory (Dovrat, Perevolotsky, & Ne'eman, 2012). Additionally, non-native plant species may be specifically targeted if they are more nutritious or abundant in the foraging habitat, or if they lack defence mechanisms from evolving without herbivory (Calvino-Cancela, 2011, Mokotjomela, Musil, & Esler, 2013). In order to manage exotic plant species it is essential to manage their dispersers. Members of the *Prosopis* family, for example, have become invasive in many regions across the globe with livestock and wildlife species acting as important dispersers of their seeds (Mworia, Kinyamario, Omari, & Wambua, 2011). Cattle are considered the species with the highest propensity to disperse *Prosopis* seeds in their dung, considering their widespread occurrence on grazing lands and herding behaviour (Shiferaw, Teketay, Nemomissa, & Assefa, 2004). However, Campos et al. (2008) suggested that exotic herbivores have different effects on the recruitment of *Prosopis* spp., as the survival and germination of ingested seeds depends on the passage through the animals' gut and the environmental conditions where the seeds are dispersed.

Considering their functional herbivory, warthogs are short-sward grazers, kneeling on their wrists to target swards close to the tiller base. It has been suggested that they might compete with other short-sward grazing species such as blue wildebeest (*Connochaetes taurinus*) and white rhinoceros (*C. simum*) but Kleynhans et al. (2011) showed that these species successfully co-exist through resource partitioning where their distribution ranges overlap. Warthogs specifically prefer grazing areas of short grasses with high N content, as well as minimal fragmentation of short grass distribution within the grazing site (Cromsigt & Olff, 2006). While ecological theory maintains that similar sized grazers are more likely to compete if resources are limited and the species' utilizes the same environment (limited spatial scales), Sitters, Heitkönig, Holmgren, and Ojwang' (2009) summarized the importance of different feeding apparatus, digestive strategy, water dependency, detoxification capacity and behavioural mechanisms of herbivores responsible for resource partitioning in African savannas. These factors reduce the risk of competition among similar sized native (blue wildebeest and zebra, *Equus quagga*) and introduced (cattle) herbivores (Voeten & Prins, 1999). For example, elephants exercise resource partitioning by increasing intake of woody plant parts such as bark, twigs and roots during hot and dry months distinguishing them from co-occurring browsing ruminants, while black rhinoceros (*Diceros bicornis*, strict browser) consume up to 20.8% more grass when co-occurring with elephants (Owen-Smith & Chafota, 2012). Similarly, warthogs might not compete with short-sward grazing livestock, such as sheep (*O. aries*), as both species may include other available plant material in their diet, and utilize different areas.

Where most livestock species movement is limited through the use of wire fencing, warthogs are able to further reduce potential competition by actively searching for resources. This was observed in populations of south-west Kenya where warthogs were more abundant on human-dominated pastoral and livestock ranches adjacent to the Mara Masai Reserve (Kenya) during the wet season, and more abundant on the reserve than on the ranches in the dry season (Bhola et al., 2012). Higher proportions of new-born piglets were also observed on ranches following the farrowing season, which coincides with the end of the dry season. Warthogs were the only small mammal species that shifted their distribution seasonally, as most small mammal species were more abundant on ranches in both seasons. The authors attributed this to the prevalence of high quality short grasses on ranches and the reduced risk of predation from ambush predators. Thaker et al. (2011) also found the odds of warthog presence increased on old agricultural lands reverting to open scrub habitats, however, their presence was also a function of predation risk by lions, leopards and African wild dogs. The presence of warthogs could potentially be beneficial for vegetation on ranch lands, as managing for livestock production modifies the ecological integrity and functioning of savannah grasslands (Tobler, Cochard, & Edwards, 2003). The co-occurrence of wild herbivores and livestock positively contribute to grass species abundance and structure (Treydte, Baumgartner, Heitkönig, Grant, & Getz, 2013) and increases landscape heterogeneity (Du Toit & Cumming, 1999, Veblen & Young, 2010). In addition, wild herbivore grazing can facilitate livestock grazing if the environment regularly experiences periods of "less stressful" conditions (e.g. productive wet season) (Odadi, Karachi, Abdulrazak, & Young, 2011).

In their native distribution range, white rhinoceros have largely been credited with the creation and maintenance of grazing lawns in savannah ecosystems, but warthogs appear to contribute proportionally more to lawn upkeep across all seasons (Kleynhans et al., 2011, Waldram, Bond, & Stock, 2008). Grazing lawns are areas characterized by the proliferation of low height-high nutritional grass species communities (Coetsee, Stock, & Craine, 2010), maintained through heavy grazing by mainly short-sward grazing species but also utilized by a variety of herbivores according to season. In the Kruger National Park these "habitat hotspots" restrict the seasonal abundance of blue wildebeest populations (Yoganand & Owen-Smith, 2014). Common lawn grasses include couch grass (*C. dactylon*), bushveld signal grass (*Urochloa mosambicensis*), lesser crab grass (*Digitaria longiflora*) and curly leaf dropseed (*Sporobolus nitens*), and are often the first to recolonize bare patches after disturbances (Van der Plas et al., 2013). Since warthogs are free-roaming they could potentially create and maintain these lawns across a mosaic landscape of agricultural and conservation areas.

2.2 Rooting

Nyafu (2009) and Smit (2014) postulated that the feeding behaviour of warthogs may have a detrimental impact on the vegetation and soil composition. Warthogs make use of rooting which is an exploratory behaviour where the soil surface is overturned in search of consumable items such as roots, rhizomes and invertebrates (Figure 4). It essentially reduces vegetation cover and increases soil exposure and aeration, which may significantly affect an environment that has evolved without similar rooting impacts. The rooting behaviour of feral pigs for example causes disparate responses among the biotic and abiotic environment of introduced habitats. Rooting by feral pigs can decrease plant species richness, diversity and biomass (Cuevas et al., 2012, Ballari & Barrios-García, 2014), modify tree regeneration structure and dynamics (Busby, Vitousek, & Dirzo, 2010), disrupt soil seed banks (Bueno, Reiné, Alados, & Gómez-García, 2011) and increase soil stored CO_2 emissions (Risch, Wirthner, Busse, Page-Dumroese, & Schütz, 2010). It can cause increased soil moisture levels, mineral contents (C and N), microbial biomass C and decreased soil compaction (Cuevas et al., 2012, Wirthner et al., 2012), and there is evidence that rooting may facilitate the invasion of exotic plant species (Tierney & Cushman, 2006, Barrios-Garcia & Simberloff, 2013). However, several studies have highlighted the influence of environmental, climatic and density-related factors on the impact and extent of rooting. Macci et al. (2012) found rooting by feral pigs degrades soil quality at high densities of feral pig populations but increases biological activity and soil organic matter quality in areas of low population densities in Mediterranean environments. In coniferous forests in northern Norway rooting by feral pigs caused minor impacts to commercial tree forests as they preferred rooting in old established forests (Haaverstad, Hjeljord, & Wam, 2014), which raises concern for the natural forest ecosystem but Macci et al. (2012) showed that anthropogenic disturbed habitats (olive groves in this study) experienced increased stress from rooting behaviour and were less efficient at protecting soil system health than natural habitats. Additionally, in mixed hardwood forests, seasonal effects overrode any effect of rooting on microbial biomass carbon or bacterial communities (Wirthner, Frey, Busse, Schütz, & Risch, 2011). Welander (2000) found that the surface area rooted varied significantly between year, season, habitat type and soil type. Larger uprooted patches occurred in the damp soils of deciduous forest floor which had overall high nutritional contents. Similarly, Elledge, McAlpine, Murray, and Gordon (2012) found areas of high quality forage material were more intensively rooted by feral pigs than areas of low forage quality in lowland coastal rainforests, and feral pigs show a preference for soil types that consist of more sand than clay soils where the sand particles are fine grained. Overall, rooting by feral pigs appears to be influenced by season (occur most often in the dry season) is dependent on soil type (damp and less compact soils) and increases with increased population density (Welander, 2000, Hone, 2002, Elledge et al., 2012, Sandom, Hughes, & Macdonald, 2013). Rooting may also be associated with the occurrence of other grazing species. Bueno, Barrio, García-González, Alados, and Gómez-García (2010) showed that in parts of feral pigs' native range, the extent and frequency of rooting events are positively associated with cattle grazing areas, rather than sheep, at intermediate stocking rates which may degrade the available grazing areas for cattle. Knowledge of the factors that influence rooting behaviour can assist in the management of populations and the development of strategies to help mitigate the associated impacts.

It is important to note that the native as well as introduced habitats of the common warthog in South Africa corresponds with the occurrence of a known native terrestrial rooting species, the Cape porcupine (*H. africaeaustralis*). It follows that these habitats would have evolved with the impacts of rooting to various degrees and might be more resilient, or even facultative dependent on the effects of rooting. Porcupine rooting has been positively associated with seedling germination and recruitment, increasing the availability of soil resources for other organisms and the creation of favourable micro-habitats (Dean & Milton, 1991, De Villiers & Van Aarde, 1994, Boeken, Shachak, Gutterman, & Brand, 1995, Bragg, Donaldson, & Ryan, 2005). They are effectively considered as ecosystem engineers that help maintain vegetation composition and biomass (Gutterman, 2003, Wilby, Shachak, & Boeken, 2001). However, porcupine and warthog rooting is functionally different; porcupines use their extended front claws to dig up below ground bulbs and tubers creating small excavations, while warthogs use their flat snout as a shovel to overturn large areas of soil surface. Considering the important implications that different types of herbivory holds for a habitat as mentioned in the previous section, warthog rooting should be considered as a major disturbance in non-native habitats and warrants in-depth investigation to determine the extent and frequency of rooting events, the plants species that are most heavily affected and might be more vulnerable to this type of disturbance, and the factors that influence warthog rooting behaviour.

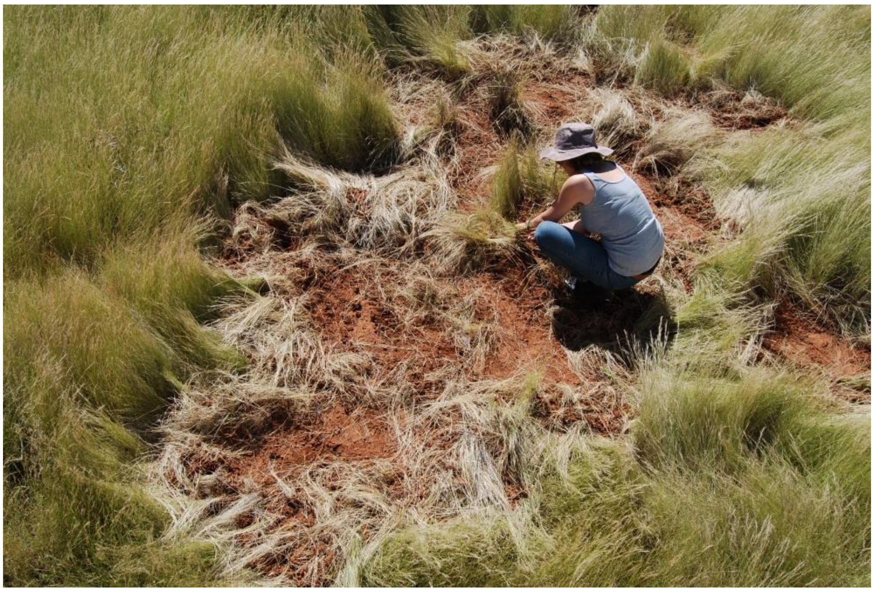

Figure 3: Rooting by warthogs in the Free State province, South Africa (Photo A. Leslie).

2.3 Crop raiding

While primary agriculture contributes a mere 3% to South Africa's gross domestic product, over 80% of the total land cover of South Africa is under some form of agricultural utilization (DAFF, 2013a). Almost 60% is classified as suitable grazing land, which harboured an estimated 13.9 million head of cattle, 21.4 million head of sheep and 2 million head of goat during the 2011/2012 production year (DAFF, 2013b). Game ranching is the fastest growing sector of the agricultural industry with approximately 16 million head of commercial game animals currently managed for game farming or in combination with livestock farming (Dry, 2012). Maize (*Z. mays*) is the largest cultivated field crop and a total of 10.8 Mt were produced in the 2011/2012 production year on 3.1 million ha of land, primarily in the central and northern regions. Other important crops include wheat (*Triticum spp*), sunflower (*Helianthus annuus*), soya beans (*Glycine max*) and sugarcane (*Saccharum officinarum*). According to O'Connor and Kuyler (2009), the cultivation of dry and irrigated crops and dairy farming have the highest relevant impact on biodiversity in South Africa, while livestock and game farming have the least relevant impact.

Due to the country's diverse topography and distribution of resources, crop, livestock and game producers are distributed across the country, while crop production is limited to areas with sufficient annual rainfall rates (only 12% of the surface land) and areas under irrigation (1.3 million ha). Crop raiding by wildlife is considered by crop producers as one of the most significant threats to crop production and yield, and carries financial as well as opportunity costs (re-sowing, crop protection). The extent and frequency of raiding is influenced by a myriad of factors, including season and extreme climatic events (floods, droughts), intensification and extension of agricultural practises, wildlife population dynamics, and crop availability and preference (Weladji & Tchamba, 2003, Linkie, Dinata, Nofrianto, & Leader-Williams, 2007, Warren, Buba, & Ross, 2007, Schley et al., 2008, Barrio, Bueno, Villafuerte, & Tortosa, 2013, Mamo, Bouer, & Tesfay, 2013). Most authors agree that the study of crop raiding has many contingencies and it is difficult to extrapolate from different study sites and among raiding species, making it difficult to assess the actual risk crop raiders pose to crop production. Feral pigs (*S. scrofa*) appear to be the exception. They tend to prefer to forage on crops rather than natural fodder when crops are available, due to the high energy content of agricultural crops (Cai, Jiang, Zeng, Li, & Bravery, 2008, Schley et al., 2008), and their diet can consist of up to 88.7% agricultural material on average, with a maximum contribution of 94% and 94.3% during the crop growing and ripening season respectively (Herrero et al. 2006).

Predator management by farmers and landowners for livestock depredation can lead to an increase in crop raiding prey densities, a contributing factor to the expansion of feral pig populations in Bhutan, with the extermination of their native predator, the dhole (*Cuon alpinus*) (Wang & Curtis, 2006). The establishment and subsequent retraction of the annual sandhill crane (*Grus canadensis tabvi*) hunting season on farmlands in Utah and Wyoming resulted in increased crane populations and crop raiding by crane, which farmers ranked the second highest pest species regarding the severity of the damage they caused to wheat fields. However, actual crop losses were determined to be less than 3% (McIvor & Conover, 1994).

The disparity between farmers' perceptions of, and actual, crop raiding events and crop raiding species is a common theme of human wildlife conflict (HWC) situations. Farmers react to crop damage according to their financial dependence on crops, the size of their land holding, length of residency and availability of compensation schemes (Hill, 2004). While the actual measurement of crop losses from wildlife raiding is difficult and controversial, and may be negligible to overall crop production and yield (Gillingham & Lee, 2003, Springer, Bowman, & Vasilas, 2013), farmers tend to overestimate crop losses. On safflower (*Carthamus tinctorius*) fields in Utah, farmers' estimation of elk (*C. elaphus*) damage was on average 5.2 times greater than the actual measured damage, as the fields are often surveyed from the edge where ungulate damage is concentrated (Haney & Conover, 2013). More conspicuous species are also disproportionately blamed for crop losses, and the low probability but high consequence raiding behaviour of these species are considered more threatening than the losses from frequent but less extreme raiders (Quirin & Dixon, 2012). At least one study reported that rodents cause more damage to crops than wildlife in northern Cameroon (Arlet & Molleman, 2007). Also, livestock and other domestic animals can cause equal or greater crop losses compared to wild animals, yet farmers fail to attribute losses to livestock, or tend to view these losses as dismissible since the benefits derived from livestock outweigh potential costs (Warren et al., 2007, Webber, 2010). Crop losses from livestock raiding are usually mitigated through compensation schemes.

In some cases, farmers complain about crop raiding species without actually experiencing significant losses themselves (Linkie et al., 2007, Karanth, Naughton-Treves, Defries, & Gopalaswamy, 2013). This can be attributed to how information is disseminated among farmers; they are more likely to interact and communicate with other members of the farming community which can influence their opinions (McIvor & Conover, 1994). However, regardless of this disparity, farmers' perceptions of wildlife damage influences their attitudes and responses towards wildlife (Conover, 1994, Wywialowski, 1994, Wang & Curtis, 2006), and should be addressed by scientists in order to mediate HWC (Hill, 2004). In Africa, the species perceived as the worst crop raiders include the elephant (*L. africana*), hippopotamus (*Hippopotamus amphibious)*, bushpig (*Potamochoerus larvatus*), feral pig (*S. scrofa*), bush buck (*Tragelaphus scriptus*) and primates (baboon and monkey spp.) (Gillingham & Lee, 2003, Kagoro-Rugunda, 2004, Mfunda & Røskaft, 2011, Nyirenda, Chansa, Myburgh, & Reilly, 2011, Chomba, 2012). Warthogs have been observed to supplement their diet with crop material, showing a preference for maize (*Z. mays*) (Figure5), and to a lesser extent wheat (*Triticum spp*.), alfalfa (*Medicago sativa*), rice (*Oryza glaberrima*), sugarcane (*Saccharum* spp.) and groundnut (*Arachis hypogaea*) (Weladji & Tchamba 2003). However, few studies have attempted to determine the factors that influence the extent and impact of crop raiding by warthogs; in some cases they are considered as major crop raiders responsible for incurring large-scale crop losses, while no crop raiding from warthogs has been reported in other cases where warthog distribution and crop production overlap.

In northern Tanzania they were observed to extensively participate in crop raiding events, which occurred mostly at night, and were succeeded only by the elephant (*L. africana*) in the extent of the damage caused (Pittiglio, Skidmore, van Gils, McCall, & Prins, 2014). They raided maize plantations during the wet season in eastern Nigeria, again mostly at night, but not during the dry season (Warren et al., 2007). They consumed mature maize cobs and also caused damage through trampling. Raiding events were also concentrated within five days of the full moon. In northern Cameroon they were held responsible for raiding maize and groundnut and to lesser extent millet plantations (Weladji & Tcamba, 2003). Important cash crops, maize, sugarcane and enset (*Ensete ventricosum*) were frequently raided by warthogs according to farmers in southern Ethiopia (Fenta 2014). Warthogs were regarded by crop farmers as the major crop raiding species among other well-known crop raiders including the elephant, anubis baboon (*Papio anubis*) and monkey (unspecified species) (Mamo et al. 2013). However, they were ranked last among perceived crop raiding species in farming areas bordering the Selous Game Reserve in Tanzania (Gillingham & Lee 2003), and while they were considered as a potential problem animal in eastern Zambia, actual crop raiding was attributed to elephants, hippopotamus (*H. amphibious)*, bushpig (*P.larvatus*) and yellow baboon (*Papio cynocephalu*) (Nyirenda et al. 2011).

Chomba (2012) also found no reports of warthog crop raiding across multiple sites in Zambia. No occurrence of warthog damage to crops was reported among farming communities bordering Lake Manyara National Park in Tanzania (Kaswamila, Russell, & McGibbon, 2007) or Lake Mburo National Park (Kagoro-Rugunda, 2004, Tweheyo, Tumusiime, Turyahabwe, Asiimwe, & Orikiriza, 2012) and Kibale National Park in Uganda (Naughton-Treves, 1998).

Members of the Suidae family are known to actively select foraging material of high quality (Harris & Cerling, 2002). It does seem that crop raiding by warthogs is influenced by more than the availability of preferred crops as is the case of the feral pig. The authors have personally observed the crop raiding behaviour of maize by warthogs (Figure 5). It appeared as if warthog(s) would move through fields trampling maize plants to bite or feed on mature maize cobs. Although most cobs were not totally consumed and with little to no significant damage, trampled plants are still experienced as losses. As the common warthog is considered a hyper grazer, it is clear that more research is required to determine their reliance on crops such as maize where these crops are available, and in the circumstance that grazing material is insufficient.

Figure 4: The damage caused to crop fields by the common warthog (*Phacochoerus africanus*) (Photo A. Leslie).

2.4 Damage to infrastructure

One of the most important negative impacts wild ungulates have on infrastructure is the damage caused to boundary and paddock fences (Kesch, Bauer, & Loveridge, 2013). Fences are constructed to contain or exclude animals within the perimeters of a property, and specifically designed according to species characteristics and behaviour (Lindsey, Masterson, Beck, & Romañach, 2012). For example, on livestock farms, fences are erected to manage the movement of livestock within the farm whilst protecting vulnerable animals by excluding predators. Conversely, on reserves and protected areas, fences are used to contain wild animals and predators from accessing human settlements or livestock farms. In South Africa, domestic and wild animals contained through adequate fencing are both a valuable and tradable commodity. Fences are costly to construct and requires regular maintenance, therefore wild animals that cause damage to fences results in a high incidence of HWC.

Warthogs are an ungulate species whose movements are not controlled through the use of conventional fences, as they either dig holes underneath or break wire strands to create openings (Kassilly, Tsingalia, & Gossow, 2008) (Figure 6a & b). Warthogs are generally not regarded as specialist burrowers as they use their snout and tusks to root and excavate burrows (Bradley, 1971), but their ability to dig large holes underneath fences using their forelegs have been observed (Schumann, Schumann, Dickman, Watson, & Marker, 2006), whilst they have been observed to cross veterinary fences in the Kruger National Park irrespective of electrical fencing and/or elephant movement, as the latter facilitates fence breaking (Jori et al., 2011). The holes they create are used by predators and smaller mammal species and animal losses are experience through predation and animal escapees (Boast & Houser, 2008). Electrical fencing were successful in managing the movements of the most important small livestock and game animal predators, namely black-backed jackals (*C. mesomelas*) and caracals (*Caracal caracal*) prior to warthog introduction (Heard & Stephenson, 1987).

According to conservative estimates the average South African farmer loses 6.35% per annum of their small livestock flock to predation by black backed jackals and caracals, which amounted to about 8,1 million animals lost to predation in the Northern Cape and 6 million in the Free State province in 2010 (De Wet, 2010). There are no numbers available on game animal losses. Maintaining the integrity of fences is therefore a priority for farmers but is compromised by the presence of warthogs. It should be noted that other major hole digging species such as the Cape porcupine (*H. africaeaustralis*) and brown hyena (*Parahyaena brunnea*) are distributed across South Africa and contribute to the creation of holes (Kesch et al., 2013); warthogs are however the only species responsible for both digging and breaking of galvanized steel and electric wires. There was a single report of warthog mortality from contact with a low-level electric trip wire on a game reserve in Limpopo province (Beck, 2008), but this was the only case found in the literature.

a b

Figure 5: a) The damage warthogs cause to fences and b) a warthog sounder moving through a fence hole (Photo a: M. Swanepoel, b: Cuddeback IR® Attack).

Vehicle accidents caused by animals crossing a road can result in vehicle damage, human injury or death, animal fatality and other financial costs such as vehicle recovery, and the loss of valuable animals (Conover, Pitt, Kessler, DuBow, & Sanborn, 1995). No comprehensive research has been undertaken on animal vehicle collisions (AVC) in South Africa, but it is estimated that they cause R 1.4 million (South African Rands) in vehicle damages annually and contributed to 8.4% of the road factors implicated in fatal vehicle accidents in 2010/2011 (Department of Transport [DAT], 2011). Installing fences next to roads can significantly reduce AVC caused by ungulates (Clevenger, Chruszcz, Gunson, Gunson, & Clevenger, 2001). Eloff and Niekerk (2005) found that 24% of all reported vehicles accidents along a 226.4 km segment of highway in the Eastern Cape province were caused by wildlife, most notably kudus (*Tragelaphus strepsiceros*), which are able to jump over conventional stock fences. Conversely, less than 1% of recorded AVC occurred along a segment where both sides of the road had game-proof fences. As mentioned, warthog movement is difficult to control through fencing, and they can cause severe motor vehicle accidents with high animal mortality rates (Mkanda & Chansa, 2011). It is expected that AVC caused by warthogs will increase if they continue to expand their range but these are likely to remain unreported, according to the Road Traffic Management Corporation (RTMC). Furthermore, the government has designated that its role in reducing AVC is improved management of the person(s) responsible for maintaining fences on private and public lands, which will have little impact on warthog movement on roads. There have been a number of incidents in Zimbabwe and other southern African countries where commercial aircrafts were damaged from colliding with warthogs on the runway. This may also continue to remain underreported where the distribution range of warthogs coincides with airplane runways.

Warthogs also expand and modify existing aardvark (*O. afer*) and porcupine (*H. africaeaustralis*) burrows which can cause vehicle accidents or damage on dirt roads or in the field. It is comparable to the effects of driving across a pothole on asphalt roadways. The enlarged burrows also pose a risk to animal safety. Livestock, especially cattle, can get stuck in burrow openings, often when lying down to calve, which can lead to injury or death of cow and/or young. If the injuries sustained are deemed too extensive to allow for recovery time or veterinary assistance, the animal is euthanized. Recently, a small number of farmers from the Free State province have reported that they have experienced livestock losses from warthog predation (Swanepoel et al., 2016., Chapter 4). According to Moreno-Opo et al. (2013) they are one of the main predators of lesser flamingo chicks (*Phoeniconaias minor*) in West Africa. Other isolated events of predatory behaviour have been reported; the hunting and killing of an ostrich chick (*Struthio camelus*) (Anonymous, 2006) in the Okavango Delta, the killing and consumption of an adult banded mongoose in Uganda (Otali & Gilchrist, 2004) and the attack but release of a new born Thompson's gazelle (*Gazella thomsonii*) in Kenya (Roberts, 2012). While common warthogs are considered strict grazers their digestive anatomy (single stomach, sharp incisors) may allow them to utilize animal material, as opposed to other herbivores (multiple chamber stomachs, flat incisors). These reports pose the question as to what extent wild suids participate in predatory behaviour. Feral pigs for example display marked levels of predatory behaviour (Ballari, Cuevas, Cirignoli, & Valenzuela, 2015). They have been found to predate on small livestock and wildlife animals (Choquenot et al., 1997, Gupta & Sinha, 2014), and consume the eggs and young of alligator (*Alligator mississippiensis*) and certain ground-nesting birds (Schaefer, 2004, Elsey et al., 2012, Carpio et al., 2014). According to Pavlov and Hone (1982), boars are more prone to prey on lambs than sows but do not predate on them at every opportunity. The authors suggested that the opportunistic scavenging of after-birth induced predatory behaviour. It has been suggested that protein deficiency during seasons marked by poorer environmental conditions drives animal predation among feral pigs (Van Vuren & Wilcox, 2009). Exotic suids may therefore pose an additional threat to domestic and native wild animals.

Wild animals also consume food sources reserved for livestock or game animals (Wambuguh, 2008). Relying on reports from farmers in the introduced regions (Swanepoel et al. 2016., Chapter 4), warthogs have been habituated to the regular feeding events of certain livestock and game animals, in which they actively participate. While these "losses" are deemed admissible by some farmers, others feel that they have a substantial impact on the amount of feed available to their animals. A simple solution would be to raise feeding troughs above ground level, out of the reach of warthogs. An experiment run by this research team found warthogs showed limited interest to selective food materials that were deliberately supplied to them at regularly frequented water troughs. This was done in light of reports from animal and crop producers that warthogs readily consume certain food items when available. The items used for the experiment included fruit (bananas, oranges, tomatoes), vegetables (carrots [*Daucus carota*], pumpkins [*Cucurbita pepo*], potatoes [*Solanum tuberosum*], sweet potatoes [*Ipomoea batatas*], sweet corn [*Z. mays* var.]), livestock feeds (lucerne based horse feed) and pig feed, dried corn, corn mixed with molasses syrup, protein material (chicken [*Gallus gallus domesticus*] eggs, raw game meat and bones [*Oryx gazella*], cooked chicken meat and bones, bone meal, domestic dog [*Canis familiaris*] pellets) (Unpublished data). Only cooked chicken meat and bones were readily consumed by warthogs, while certain items elicited varying levels of curiosity, including sweet corn, dried corn, bone meal and raw game meat and bones. It is suggested that warthogs consume certain articles if they have become accustomed to its regular availability i.e. it is a learned behaviour.

On farmlands warthogs frequently bath in water troughs (Figure 7) and may damage the mechanisms that regulate water levels. After bathing they wallow in the mud pool around the trough and sometimes climb back into the trough, muddying the water. (Bracke, 2011) concluded that mud wallowing and bathing behaviour of pigs is most likely for thermoregulation, but also discusses the possibility that they wallow for personal pleasure, similar to dustbathing in poultry. Interestingly, mud wallowing and subsequent rubbing against trees act as a vector of transport for freshwater invertebrates, an important activity also performed by buffalo (*Syncerus caffer*), rhino and elephant (Vanschoenwinkel et al., 2011).

Figure 6: The common warthogs (*Phacochoerus africanus*) frequently bathe in water troughs (Photo: Cuddeback Attack® IR).

Warthogs are also held responsible for digging up and damaging plastic irrigation pipes although porcupines are generally considered responsible for damaging pipes (Chevallier & Ashton, 2006), and have been observed to unearth and damaged the subsurface fibre-optic cables at a copper mine (Anonymous, 2002). In warthogs, the upper canine is long and curved and used for rooting while the bottom canine becomes razor sharp from constant grinding. These are formally referred to as "tushes" and used for intra-species fighting, but they may pose a risk to humans if injured or cornered although incidents are rare or possibly underreported.

2.5 Diseases

Warthogs may carry or be susceptible to a range of different infectious agects which may affect domestic livestock or humans. Some of these diseases are of major importance to the agricultural and public health sector since they cause production and financial losses, including mortalities among livestock animals while zoonotic diseases may infect humans and cause debilitating illness or death. Introduced gemsbok (*Oryx gazella*) in New Mexico is implicated in disease exposure responsible for increased mortality among native ungulate species (Marquez & Boecklen, 2010). A comprehensive review of these diseases and their associated risks has been conducted in Chapter 3.

3 Feral pig management and damage mitigation

Feral pigs (*S. scrofa*) are considered among the most invasive species in the world (Lowe et al., 2000, Perez, 2005, Nogueira, Nogueira-Filho, Bassford, Silvius, & Fragoso, 2007, Hartley, 2010, Elledge et al., 2012). They were introduced to the Western Cape of South Africa but curiously enough have not been able to invade in a similar fashion to their Australian counterparts, although they are considered as Category 1 b invasive species defined as "invasive species that require control by means of an invasive species management programme" (DEA, 2014). Small and relatively isolated populations do occur in and outside of the reserves in the Western Cape, but it appears as if certain biogeographical factors have been limiting their establishment and spread. Recently however, conservation authorities have started to survey and manage populations on agricultural lands in regions where they raid vineyards and apparently predate upon ground nesting bird and small animals including the endangered geometric tortoise (*Psammobates geometricus*) (Fincham & Hobbs, 2013). In other places of introduction, feral pigs have been responsible for native species extinctions, predation, habitat alteration, and disease transmission (Barrios-Garcia & Ballari, 2012). Considering the major impacts associated with introductions, they are subjected to control and monitoring programs in most countries that form part of their introduced and native range. However, their population dynamics and environmental adaptability renders the species difficult to control. This is further exasperated by the ongoing illegal transportation and introduction of feral pigs (Spencer & Hampton, 2005). Massei, Sugoto, and Bunting (2011) summarized the lethal and non-lethal methods to manage feral pigs, concluding that effective management operations are tailored to the target species, combine different control methods, and should establish monitoring programs to measure outcomes.

According to Dolbeer (1998), lethal management is the most effective strategy to control damage-causing vertebrate species where the population status and dynamics of a species allows it, alternative control strategies are impractical or less efficient, and the outcomes of management, including reduction in damage, is measureable. Although modern society prefer non-lethal methods for wildlife control, the public tend to support lethal control when a situation warrants it, which increases with the severity of damage experienced (Wittmann, Vaske, Manfredo, & Zinn, 1998, West & Parkhurst, 2002, Koval & Mertig, 2004). Geisser and Reyer (2004) investigated the effectiveness of hunting, feeding and fencing to reduce crop damage (*S. scrofa*), and concluded hunting to be the only effective control strategy. Both aerial and ground hunting is used to reduce population numbers and mitigate negative impacts, and have been successfully applied to eradicate pigs from an area (Parkes et al., 2010, Barron et al., 2011). Hunting by humans accounted for the majority of pig mortalities in central Europe, which highlighted the importance of human induced mortality in a highly productive mammal species (Keuling et al., 2013). Hunting is considered a simple and effective control method with the added benefit of producing meat (Parkes & Murphy, 2003). However, these operations are only effective if they are applied consistently across succeeding seasons, as pigs are quick to immigrate to cleared areas, reproduce rapidly and become re-established (Barron, Anderson, Parkes, & 'Ohukani'ohi'a Gon III, 2011, Engeman et al., 2014). It has been noted that opportunistic and recreational hunting maybe inefficient if it is predictable and biased towards age, sex, timing, and more conspicuous individuals (Festa-Bianchet, 2008), while vehicles and helicopters 'expose' hunters to early detection (Cromsigt et al., 2013) which animals learn to elude (Thurfjell, Spong, & Ericsson, 2013).

Therefore, Festa-Bianchet (2008) advocated that hunting as an artificial management approach should attempt to mimic natural mortality, which requires a sound understanding of a species' population dynamics and interaction with the environment. Natural mortality among wild boar is primarily governed by climatic conditions and resource availability (Massei, Genov, Staines, & Gorman, 1997), with the mortality rate highest during the first (48%) and second (69%) year of life (Jezierski, 1977). Therefore it has been suggested that hunters focus their efforts on piglets and juveniles, and sows in general, for effective population reduction and control (Bieber & Ruf, 2005, Servanty et al., 2011, Gamelon et al., 2012, Keuling et al., 2013). Bieber and Ruf (2005) found the primary drivers of population growth, namely juvenile fecundity and survival, are significantly affected by environmental conditions and suggested that hunting efforts accommodate environmental changes to optimize population control. According to the authors, population reductions would be most effective by high hunting pressure on juveniles during periods of optimal environmental conditions. Conversely, hunting adults during periods of sub-optimal environmental conditions would be more effective in population reduction as variable climatic conditions directly influences habitat quality and resource availability, and in turn the measures of ungulate body condition and weight (Post & Stenseth, 1999). This may be difficult to achieve as younger individuals are smaller and less conspicuous, form smaller targets and generally illicit sympathy from hunters (Festa-Bianchet, 2008, Keuling et al., 2013).

Cromsigt et al. (2013) suggested the novel approach of 'hunting for fear', where hunting events aim to elicit a behavioural response in pest animal populations to avoid areas of high human-wildlife conflict. It is based on the theory that spatial distribution of African ungulates is a function of the predation risk from large or primary predators, as illustrated by Thaker et al. (2011). Control methods should consequently increase temporal randomness but retain spatial consistency of human hunting to influence ungulate spatial distribution. However, the authors (Cromsigt et al, 2013) note that hunting methods tailored to induce stress and fear among ungulates is likely to receive a negative public response, and potentially create conflict between conservation and economic incentives. As a result, non-lethal methods have become increasingly popular due to public scrutiny of lethal methods (Reiter, Brunson, & Schmidt, 1999). However, hunters or persons with family members that hunt are more willing to support and participate in wildlife management, and more likely to consume game meat (Radder & le Roux, 2005, Ljung, Riley, Heberlein, & Ericsson, 2012, Golden, Peterson, De Perno, Bardon, & Moorman, 2013). Combining different hunting methods, including so-called 'non-lethal hunting for fear', might allow for wildlife management approaches that aim to integrate ecological and human interests in wildlife management, and encourage sustainable wildlife utilization and thereby conservation efforts.

The use of traps to capture and retain feral pigs for translocation or euthanasia has been applied as singular control or in combination with other methods. Different trap designs have unique advantages and disadvantages and are used to achieve specific management goals. Corral traps for example are considered more efficient as they trap more pigs per trap night at a lower cost than box traps (Williams, Holtfreter, Ditchkoff, & Grand, 2011). The use of traps garners more public support but is generally less efficient than lethal methods (Koichi, Cottrell, Sangha, & Gordon, 2013). Other major drawbacks of the method are that it is labour intensive, time consuming, expensive and biased towards certain cohorts, while animals become trap wary over time (Choquenot, Kilgour, & Lukins, 1993, Hanson et al., 2009, Williams et al., 2011). Translocation instead of euthanasia is only effective in reducing populations when local food resources are limited and immigration is prevented (Massei et al., 2011). This method is impractical and illegal in many countries where the species is non-native, as translocated animals can become problem animals in their introduced range. There is also the risk of introducing novel pests and pathogens.

Species-specific baiting has been used to increase the efficiency of culling events. Feral pigs tend to modify their distribution range to include bait stations and spend proportionately more time within this area (Campbell et al., 2012). Baiting stations and permanent water points serve as opportunistic stations to observe animal behaviour and allow for predicting patterns for culling activities. Poisoned baits have proved to be very effective for controlling feral pigs in Australia (Hone & Stone, 1989, Hone, 2002) but poisoning wildlife is illegal in many countries across the globe due to public sentiment and the associated environmental risks. The direct or secondary poisoning of non-target wildlife species has caused devastating losses among wildlife populations, including highly endangered species (Guitart et al., 2010, Chaudhry, Ogada, Malik, Virani, & Giovanni, 2012). Although it is illegal to poison wildlife in 38 of 46 African countries (83%), including South Africa, it is still widely practised for damage animal control and bushmeat production (Ogada, 2014). Carbofuran, a highly toxic carbamate pesticide, is the most commonly used poison in Africa for wildlife species, including 'nuisance' warthogs.

Non-lethal control methods have become increasingly popular due to public scrutiny of lethal methods (Reiter et al., 1999) but are usually costly, labour intensive and only effective on certain species or populations. Fencing is a common tool used to manage feral pig movement, including containing to or excluding them from an area (Hone & Atkinson, 1983). It has allowed for the swift eradication of populations in a sufficiently fenced area through intensive trapping and hunting programmes (McCann & Garcelon, 2008). There are different types of simple fences with varying degrees of effectivity, including the use of electric fencing. Geisser and Reyer (2004) found electric fencing to be ineffective in minimizing crop damage despite many other studies finding it highly effective. Reidy, Campbell, and Hewitt (2008) tested different electrical fence designs and found a fence with two electrical wire strands, at 20 and 45 cm from the ground, excluded 75% of visiting hogs. They concluded that while no type of electrical fence is 100% feral pig proof, it can significantly restrict their movement and subsequent damage to crops.

Alternatively, Day and Macgibbon (2007) maintained that fences should act as a physical barrier for target species. Lavelle et al. (2011), constructed enclosures (20x40 m) using 0.86 m high hog panels, and concluded these to be very effective, inexpensive and easy to construct. It is however not economical and practical to use hog panels for containing or excluding feral pigs from large tracts of land such as farms and ranches. Taken as a whole, fencing has important ecological, financial and social implications as outlined in the review by Lindsey et al. (2012), and the construction of fences for wildlife management should consider all the possible negative impacts on the ecosystem and its inhabitants. For example, a number of reptilian, amphibian and mammalian species are susceptible to electric fence induced mortality (Long & Robley, 2004, Beck, 2008). It is one of the major threats for Temminck's ground pangolin (*Smutsia temminckii*), listed as vulnerable in South Africa and protected in Namibia, Botswana and Zimbabwe (Pietersen, Mckechnie, & Jansen, 2014).

The use of repellents and deterrents to protect crops are effective for only short periods of time as animals become habituated to these methods. Supplementary and diversionary feeding has been used to divert animals' attention from protected resources such as crops (Calenge, Maillard, Fournier, & Fouque, 2004), but the efficacy of this method remains inconsistent. Furthermore, additional feeding is not proposed as a management method for feral pigs as it can alter long term population dynamics (Bieber & Ruf, 2005), increase population growth and survival (Frackowiak, Gorczyca, Merta, & Wojciuch-Ploskonka, 2013) despite limiting climatic factors (Oja, Kaasik, & Valdmann, 2014) and potentially increase or cause additional negative impacts (Geisser & Reyer, 2004). Feral pigs show no or slight avoidance behaviour for deterrents such as noise disturbance, illumination of bait stations (Bengsen, Leung, Lapidge, & Gordon, 2010), solar powered LED blinkers or odour/gustory repellents (Schlageter & Haag-Wackernagel, 2012a, b). Schlageter and Haag-Wackernagel (2011) suggest that wild boars respond very cautiously to changes in their habitat, but there is no evidence of deterrence from neophobia. Pro-active guarding of valuable crops by humans is considered as the easiest and most effective method to reduce crop damage by feral pigs (Warren et al., 2007, Cai et al., 2008), but it is time consuming, tedious, and can lead to a loss of income or transmission of zoonotic diseases (Tweheyo et al., 2012).

Cai et al. (2008) suggested that farmers decrease their dependence on crops for financial income, and whilst this might be possible for rural farmers, it does not apply to commercial farms. Rural farmers might become more dependent on the environment and increase bushmeat consumption, which surprisingly, may have positive outcomes if the pest species is the target of hunting efforts. In oil plantations in Indonesia, hunting of feral pigs for crop damage reprisal has spawned a commercial market for the meat which feeds back into feral pig management (Luskin, Christina, Kelley, & Potts, 2014). Similarly, feral pigs have become the major target of bushmeat hunters in the Brazilian Pantanal, serving as a replacement for the overall heavily hunted native species (Desbiez, Keuroghlian, Piovezan, & Bodmer, 2011). The idea of promoting human consumption of invasive species as a means of control has previously been suggested (Roman, 2005), although Nuñez, Kuebbing, Dimarco, and Simberloff (2012) debated that this approach should be carefully evaluated since it can create a market that needs to be sustained, and also facilitate the expansion of invasive populations or promote further introductions. However, in certain cases the ecological and socio-economic conditions required for eradication of a pest species as set out by Bomford and O'Brien (1995) might not be present, and active control is required to control population growth and dispersal (Hone, 2002).

4 Game meat production and quality

As an alternative to the bushmeat industry, the formal production of meat from wild animals has been suggested as a low-input, high production alternative to traditional animal husbandry (Carruthers, 2005, Van Schalkwyk, McMillin, Witthuhn, & Hoffman, 2010, Kiley-Worthington, 2014). Compared to domestic livestock, wild herbivores are more efficient at converting feed, more resistant to endemic pests and pathogens, less water-dependent and more adapted to climatic extremes (Child, Musengezi, Parent, & Child, 2012, Lindsey et al., 2013). In semi-arid rangelands, farming with wildlife or practising eco-agriculture promotes ecosystem biodiversity and health; where wild herbivores co-occur with livestock they positively contribute to grass species abundance and structure (Treydte et al., 2013), increase landscape heterogeneity (Du Toit & Cumming, 1999, Veblen & Young, 2010) and facilitate livestock grazing (Odadi et al., 2011). Promoters of game meat consumption maintain that utilizing wild animals contributes towards sustainable wildlife and habitat management, and local food security, while generating an income from a widely available resource (Barnes & de Jager, 1996, White & Lowe, 2008, Poshiwa, Groeneveld, Heitkönig, & Prins, 2013, Chaminuka, Udo, Eilers, & van der Zijpp, 2014). Game farming is an important industry in many developing countries (Saadoun & Cabrera, 2008) while sustainable meat production systems is considered an inevitable future outcome for the meat industry (Kristensen, Støier, Würtz, & Hinrichsen, 2014).

It is important to note that the promotion of game meat for human consumption is based on the premise that the meat is harvested from wild animals in a sustainable manner and the wild populations are managed to promote growth and stability. This type of harvesting is not similar to bushmeat hunting in parts of Africa where certain animal species are intensely and illegally hunted by humans for food, which has caused local species extinctions or severe reductions of distribution ranges (Hoffman & Cawthorn, 2012). Game meat destined for the formal market is produced by farms and reserves that farm with or hunt wild animals, and is also a by-product of hunting for recreation, population management or problem animal control purposes. Foreign and local hunters pay to hunt ungulate species for biltong production (a type of South African dried meat product) and trophy animals on ranches and reserves. These two activities generate the most revenue, while fresh game meat production only generates a small portion of the total income. In Namibia, safari hunting accounts for the majority of game meat produced (Van Schalkwyk et al., 2010). More than 95% of the game meat produced annually (between 15 917 000 and 24 952 000 kg) is consumed within the country allowing for 87% of livestock meat produced to be exported. During the six month hunting season, game meat contributes approximately 10% of red meat utilized per annum in South Africa, which was estimated at around 1 249 000 kg during 2011/2012 (Dry, 2010, DAFF, 2013b).

Although consumers and producers have become increasingly aware of the health attributes of game meat in general and its value as a sustainable red meat source (MacMillan & Phillip, 2008), it has been suggested that general ignorance regarding the quality aspects of game meat and preparation methods has been crippling the growth of the fresh game meat industry. The visual appearance of meat and meat products is one of the most important factors relating to consumers' expectations and willingness to purchase. Through visual perceptions consumers assess quality, freshness and eating sensation (Font-i-Furnols & Guerrero, 2014) and discern for an attractive colour and reduced levels of visible fat. The appearance of game meat colour has been considered unattractive by consumers (Volpelli, Valusso, Morgante, Pittia, & Piasentier, 2003, Hoffman & Wiklund, 2006, Hoffman, Kroucamp, & Manley, 2007a, Hoffman & Laubscher, 2010). However, game meat is also considered exotic, which is attractive to consumers who are adventurous and pursue new culinary experiences, and to foreign tourists who want to consume meat from native animals (Crafford, Muller, & Schutte, 2003, Hoffman, Muller, Schutte, Calitz, & Crafford, 2005) or take meat products home as souvenirs. Exotic meat also enjoys the interest of the social elite where it is marketed in affluent restaurants as a highly valued, and priced, commodity (Adams, 2000). Burger (2002) found that demographic factors including gender, ethnicity and household income influences the amount of wild game meat and fish consumed among North American consumers. Overall, men consume more game and wild-caught fish than women, while black consumers consume more wild-caught fish than game, and wealthy households consume more deer than other game meat species. Black consumers were more concerned about the “strong flavour” of game meat, while white consumers ate more game meat, and associated the meat with health benefits.

Koster, Hodgen, Venegas, and Copeland (2010) found hunters tended to prefer animal species they associate with an appealing flavour, and may therefore only hunt and consume the meat of a smaller number of species than those available to them, or only hunt those they are familiar with. In South Africa, the most popular species hunted include gemsbok, blue wildebeest, common eland (*Taurotragus oryx*), kudu and impala (*Aepyceros melampus*) (Warren, 2011), while the most frequently consumed species include springbok (*Antidorcas marsupialis*), kudu and warthog (Hoffman et al., 2003). Hoffman et al. (2005) found that South African consumers positively associate game meat with leanness, healthiness and typical game flavour, and negatively with price, availability, and typical game flavour. Since meat consumption is primarily influenced by availability, price and tradition (Bender, 1992), educating consumers on the quality characteristics and preparation of game meat is necessary to encourage game meat consumption.

The meat from wild animals has often been sold under collective terms of ‘game meat’ and ‘venison’. However, a number of studies contended that game meat should be classified and marketed according to species and rearing system (wild or farmed) considering the significant differences in fatty acid composition and associated sensory characteristics (Rødbotten, Kubberød, Lea, & Ueland, 2004, Hoffman, Mostert, & Laubscher, 2009c, Valencak, Gamsjäger, Ohrnberger, Culbert, & Ruf, 2015). Furthermore, game meat should be produced according to international quality and safety standards to promote its utilization globally (Bekker, Hoffman, & Jooste, 2012, Hoffman, 2015). The recommendations made by Van der Merwe, Jooste, and Hoffman (2012) include the following; earlier introduction and maintenance of the cold chain, implementing and practising Good Hygiene and Good

Manufacturing Practices, improving shot placement and evisceration techniques, and reducing the risk for microbial contamination.

In general, game animals produce a lean and healthy meat, which is high in protein, low in fat with a favourable fatty acid profile. Game meat is valued for its leanness, exoticness and gamey flavour (Hoffman & Wiklund, 2006), but may vary in quality since it is not traditionally "farmed" where animals are closely controlled to produce meat of a certain standard. Scientific literature has highlighted the superior carcass and meat quality parameters of game animals (Van Zyl & Ferreira, 2004, Mostert & Hoffman, 2007, Hoffman, Kroucamp, & Manley, 2007b, Hoffman, 2008, Hoffman, Smit, & Muller, 2008, Dannenberger et al., 2013, Bartoň, Bureš, Kotrba, & Sales, 2014). Other than domestic species, wild ungulates develop under variable conditions with genetic and environmental factors influencing body weight, muscle acquisition, fat deposition, and bone formation. Subsequently, the carcass yields and dress out percentages of wild ungulates vary according to species, geographic range, season, age, sex and plane of nutrition (Taylor, Skinner, & Krecek, 2005, Hoffman, Mostert, Kidd, & Laubscher, 2009a, Hoffman, Van Schalkwyk, & Müller, 2009b). Wild herbivores are dependent on the habitable environment to satisfy their physical and nutritional needs. Periods of nutritional stress such, as experienced during times of drought or extreme cold, result in poorer carcass yield and meat quality. However, the current game farming industry in South Africa is moving towards a more controlled management system, using fences, predator control, breeding programs and supplementary feeding (Mysterud, 2010) to produce a high quality meat of a consistent standard, according to consumer preferences.

Since fresh game meat is generally sold as whole cuts or as a combination of muscle groups, studies have aimed to investigate and characterize the physical and chemical qualities of game animal muscles. Skeletal muscles are a filamentous, multinucleated combination of heterogeneous myofibres which differs in metabolic and contractile characteristics, while muscle fibre type and composition is influenced by species, sex, plane of nutrition and maturity, and environmental factors in the case of free ranging animals (Keeton & Eddy, 2004). Muscle mass is related to total number of fibres (TNF), myofibre cross section area (myoCSA) and length of myofibres, and there is greater variation among species regarding the TNF than myoCSA of individual muscles, which also appears to explain muscle sizes in dimorph species (Rehfeldt, Stickland, Fiedler, & Wegner, 1999). The differences in physical and chemical characteristics determine palatability and therefore consumer enjoyment and acceptance (Jeremiah, Dugan, Aalhus, & Gibson, 2003). In living muscle, glucose and oxygen are converted to usable energy with water and carbon dioxide as by-products. As the animal is slaughtered and exsanguinated, the circulation of oxygen to the muscles ceases while glycogen continues to be converted to glucose anaerobically, with lactic acid and water as by-products. This significant build-up of lactic acid in the muscles is quantified by measuring the rate of pH decline (Honikel, 2004). Muscle pH is one of the most important parameters to manage for in meat production, as it affects colour, flavour, tenderness, water holding capacity and shelf life of the final product, which ultimately determines eating quality and consumer acceptance.

The pH of living muscles range from 7.0 to 7.2 which decreases post mortem to reach the ultimate pH (pH_u). The pH_u is influenced by genetics, breed, sex, muscle type and muscle fibre type, pre-slaughter stress and post-slaughter handling, as well as environmental effects such as season, while variation in pH_u affects the tenderness, colour, water-holding capacity and ageing process of meat (Honikel, 2004). At 24 hours post mortem the desirable pH_u of meat should range between 5.3 and 5.8, as a low pH_u retards microbial growth and imparts flavour components. According to England, Matarneh, Scheffler, Wachet, and Gerrard (2014), a pH of 5.5 inhibits the glycolytic enzyme phosphofructokinase and post mortem glycolysis which may explain the similar ultimate pH of meat from different species. A higher ultimate pH_u results in meat that appears dark, firm and dry (DFD) as pertaining to its meat quality. DFD meat has a high final pH due to the low concentrations of glycogen at the time of slaughter, reducing the capacity for post mortem acidification. The meat has increased water-holding capacity with a higher risk of spoilage due to an increased susceptibility for micro-organisms (Lawrie & Ledward, 2006), while more precisely, the lack of carbohydrates selects for a proteolytic flora instead of a largely carbohydrate-dependent lactic acid bacteria dominated flora (Kraft, 1992). In pale, soft and exudative (PSE) meat, the accelerated pH decline post-mortem combined with high temperatures leads to the denaturation of proteins, and the meat becomes pale in colour, soft in texture and has decreased water-holding abilities (Monin, 2004). Both phenomena are associated with the meat from animals that experienced ante-mortem stress. Stress results in the release of stress hormones epinephrine and norepinephrine into the blood stream, which stimulates the rapid breakdown of muscle-stored glycogen to glucose prior to slaughter.

Wounded animals, or animals that have been pursued for a great distance, are subjected to stress resulting in the depletion of glycogen reserves and compromised meat quality. Hoffman and Sales (2007) noted similar PSE characteristics in warthog meat when subjected to ante-mortem stress. Some studies found pre-slaughter stress to have a negligible effect on the meat quality parameters of reindeer (*Rangifer tarandus*) (Wiklund, Andersson, Malmfors, & Lundström, 1996), red deer (*C. elaphus*) (Pollard et al., 2002) and pH decline in wild boar (*S. scrofa*) (Marchiori & Felício, 2003). Daszkiewicz, Janiszewski, and Wajda (2009) agreed with others that meat from wild animals has lower pH_u possibly from increased post mortem lactic acid production compared to domestic animals. In support, a review of African game meat profiles found no species to have attained a pH_u of > 5.9 when there have been minimal levels of ante-mortem stress (Onyango, Izumimoto, & Kutima, 1998, Kritzinger, Hoffman, & Ferreira, 2004, Rincker & Bechtel, 2006, Hoffman et al., 2009a, b, Hoffman & Van Schalkwyk, 2011, Magwedere, Sithole, Hoffman, Hemberger, & Dziva, 2013).

Environmental effects such as season can also influence pH_u, with some studies finding a higher pH_u in the meat from domestic (cattle, goat and sheep) collected in the hot season (Kadim et al., 2004, 2008). Seasonal variation in pH_u of wild animals is likely caused amongst others by a combination of ambient temperatures and reproductive activities. For example, high environmental temperatures may impair energy utilization and reduce feed intake, and together with increased physical exertion during the mating and farrowing season, contribute towards decreased glycogen muscles stores and higher post-mortem pH_u values (Immonen, Ruusunen, Hissa, & Puolanne, 2000, Kadim et al., 2004). Conversely, wild ungulates in good body condition with high nutrition status have increased glycogen muscle content which results in increased post-mortem lactic acid production and low albeit normal pH_u (Wiklund et al., 1996).

A number of studies have investigated the water holding capacity (WHC), cooking loss and drip loss of game meat with different results regarding the influence of species, sex, harvesting season and culling method. The WHC, cooking and drip loss values are usually significantly correlated with pH_u of meat (Bouton, Harris, & Shorthose, 1971), with pH_u and WHC considered significant indicators of drip loss, or exudative meat (Kušec, Kralik, Đurkin, Petričević, & Hanžek, 2007). Post mortem moisture loss occurs following changes in the muscle cell and myofibrilar structure and increased protein denaturation as pH declines. It becomes greater as pH approaches the isoelectric point (≈ 5.5), and when rapid pH decline occurs at high temperatures with onset of rigor. Other than the effect of pH and temperature, there is also evidence that ionic strength and protein oxidation affects the ability of fibres and fibre bundles to hold water (Huff-Lonergan & Lonergan, 2005). A positive relationship between pH_u and WHC has been found in numerous game species (Onyango et al., 1998, Hoffman et al., 2009c), while other authors found wild boars have lower drip loss and WHC ratios compared to domestic swine (Marchiori & Felício, 2003, Szmańko, Górecka, Korzeniowska, Malicki, & Eeremenko, 2007). A favourable drip loss is < 5% as a drip loss > 5% is generally associated with PSE pork (Van der Wal, Bolink, & Merkus, 1988). The ability of meat to retain water influences raw and cooked product weight, protein content, tenderness and eating quality.

The meat from wild animals appears to have a higher initial tenderness compared to beef (Farouk et al., 2007, Hoffman et al., 2007a, Hoffman, Smit, & Muller, 2010, Wiklund, Dobbie, Stuart, & Littlejohn, 2010, Daszkiewicz, Kubiak, Winarski, & Koba-Kowalczyk, 2012, Sales & Kotrba, 2013), but the mechanisms involved are even less understood for wild than domestic animals. It has been suggested that post mortem proteolysis occurs at a faster rate in the muscles from game animals from the earlier activation of calpain I and calpain II post mortem compared to beef (North, Frylinck, & Hoffman, 2015, 2016). While the collagen content in raw meat correlates well with meat toughness, the contribution of connective tissue to meat tenderness decreases as cooking temperature increases (Aaslyng, Bejerholm, Ertbjerg, Bertram, & Andersen, 2003). At internal core temperatures of ≥ 80°C collagen becomes gelatinous, resulting in a decreased toughness in muscle cuts high in connective tissue. Conversely, muscles with low connective tissue become tougher likely due to increased myofibrilar toughness from actin denaturation (Bejerholm & Aaslyng, 2004). According to Purslow (2005), the background toughness of meat is largely attributed to variation in the amount of perimysium rather than endomysium among different muscles. The perimysium is responsible for determining muscle fibre size which has been negatively associated with meat tenderness, as shown by Taylor, Labas, Smulders, and Wiklund (2002) for moose and reindeer meat. As muscles grow and mature, there is an increase in the amount of non-reducible cross-links of the collagen resulting in a decrease in collagen breakdown, which along with an increase in the insolubility of the muscle elastin, contributes to the overall increase in meat toughness with age (Karlsson & Klont, 1999, Purslow, 2005, Dai et al., 2009).

Other than intrinsic factors (muscle fibre and collagen composition), post-mortem handling and carcass chilling, e.g. rate of temperature and pH decline during the onset of rigor mortis, influence muscle tenderness (Maltin, Balcerzak, Tilley, & Delday, 2003). In general, tender meat is associated with a normal rate of pH decline within the desired temperature range of 10–15°C with the onset of rigor. Low pH_u values around 5.5 have been positively associated with increased tenderness compared to intermediate pH_u values ranging from 5.8-6.0 for game meat (Hoffman et al., 2007a, Wiklund et al., 2010) and beef (Lomiwes, Farouk, Wu, & Young, 2014). However, Wiklund et al. (2010) found that lower pH_u values decreased colour stability and shelf life.

Meat colour develops post mortem as muscle myoglobin is oxygenized to oxymyoglobin when freshly cut meat is exposed to atmospheric oxygen (Mancini & Hunt, 2005). Myoglobin quantity and quality varies with muscle fibre composition, muscle type, animal age, diet and exercise (Lawrie & Ledward, 2006), whilst colour development is influenced by pH decline, temperature, rate of metmyoglobin reduction, rate of oxygen consumption and lipid oxidation (Mancini & Hunt, 2005, Faustman, Sun, Mancini, & Suman, 2010). Game meat is typically considered a red meat due to high levels of myoglobin in wild animal muscles (Onyango et al., 1998), which is contributed to elevated activity or exercise levels of wild compared to domestic animals (Daszkiewicz et al., 2012). Muscles generate energy through an oxidative or glycolytic metabolic pathway with the myoglobin contents differing according to their function. Myofibres with an oxidative metabolism require high quantities of myoglobin to supply and store oxygen for periods of slow contraction activity. These muscles are mainly used for sustained low intensity activities and should theoretically comprise of a larger proportion of oxidative rather than glycolytic metabolic myofibres. Myofibres with an anaerobic metabolism use stored glycogen for energy during periods of fast contraction activity. Since glycolysis occurs anaerobically, low levels of myoglobin is present and the myofibres appear lighter and less red. In general, mammalian hindquarter and loin muscles are responsible for fast and extreme movements

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and stability and will be lighter (Choe et al., 2008, Hyytiäinen, Mykkänen, Hielm-Björkman, Stubbs, & McGowan, 2014, Kang et al., 2011). According to Faustman et al. (2010), muscles comprised of more red fibres are higher in intramuscular fat (IMF) in the form of triglycerides, and in myoglobin and iron, with greater oxygen consumption rates which makes them more susceptible to discolouration and lipid oxidation. In addition, higher pH_u values are linked to darker and redder meat colour from the increased association between protein and water molecules resulting in more light being absorbed, while lower pH_u values increase the release of water from denatured proteins, making excised muscle appear more superficially wet and lighter due to light being more readily reflected.

Myoglobin levels, nitrogen, total fat, intramuscular fat content, fatty acid profile and enzymatic functions differ among animal muscles and species, which changes with age and maturation (Lawrie & Ledward, 2006). The differences determine preparation methods, palatability, and ultimately consumer acceptance (Jeremiah et al., 2003). The general chemical composition of game meat agrees with that denoted to lean meat, which constitutes of > 70% moisture, > 20% protein, < 3 % fat and approximately 1% ash (minerals) content (Dannenberger et al., 2013, Hoffman et al., 2009b, Hoffman et al., 2007b, Hoffman et al., 2010). As meat is an important source of protein and amino acids, the total crude protein content and amino acid profile are characteristics pertaining to the nutritional quality of meat (Higgs, 2000). The average crude protein content for raw red meat is 20-25g per 100g, and contains all the essential amino acids; lysine, threonine, methionine, phenylalanine, tryptophan, leucine, isoleucine and valine (Keeton & Eddy, 2004).

Total fat content is inversely related to both total moisture and protein content in the meat from domestic animals i.e. with increasing fat content the content of moisture and protein decreases. However, as noted by Neethling, Hoffman, and Britz (2014), the overall low fat content of game meat appears to amplify the relationship between moisture and protein content. This means that the overall moisture and lipid content increased as the protein content decreased. Wild animals have a higher muscle to fat ratio compared to livestock animals, are less prone to depositing subcutaneous fat than intra-muscular fat, and have a more favourable fatty acid profile, with an increase in the proportion of poly-unsaturated fatty acids to saturated fatty acids. The low overall lipid content and fatty acid composition is primarily attributed to their forage diet and high levels of activity (Valencak & Gamsjäger, 2014) however, the large variation in IMF content of wild boar *Psoas major* muscle was attributed to diet and not sex or maturity (Quaresma et al., 2011). Increased fat deposition and intramuscular content follows an increase in the plane of nutrition and/or age of the animal. In terms of sex, lower levels of IMF and subcutaneous fat has been found for male springbok (Hoffman et al. 2007b), impala (Hoffman, 2000), blesbok (Neethling et al., 2014), roe deer (Daszkiewicz et al., 2012) and red deer (Daszkiewicz et al., 2009). It has been suggested that reproductive expenditures is responsible for the lower fat levels following the rut season of male impala (Hoffman, 2000), blesbok (Kroon, Van Rensburg, & Hofmeyr, 1972), and red deer (Stevenson, Seman, & Littlejohn, 1992), and the low bodily fat indexes of mountain reedbuck (*R. fulvorufula*) (Taylor et al., 2005) and common eland (Von la Chevallerie, Erasmus, Skinner, & Van Zyl, 1971).

The major and most abundant fatty acids (FA) found in animal meat are palmitic and stearic (saturated) and oleic (monounsaturated) fatty acids (Enser, Hallett, Hewitt, Fursey, & Wood, 1996). However, the FA composition varies with total carcass fat content and muscle type, which is influenced by species, genetics, diet, animal age, sex, exercise and season (Wood et al., 2008, Dannenberger et al., 2013, Neethling et al., 2014). Monogastric animals such as pigs have a higher proportion of polyunsaturated fatty acids in muscle and adipose tissue as these FA passes unchanged through the gastric system to be incorporated. The majority of unsaturated FA is rapidly biohydrogenated to saturated FA (SFA) by rumen microbes, and therefore occurs in lower proportions in muscles (Jenkins, 1993, Wood et al., 2008). However, the meat from wild or free ranging animals have a higher polyunsaturated FA (PUFA), and n-3 in particular, content (Valencak & Gamsjäger, 2014), as animals extensively feeding on grasses incorporate more n-3 and n-6 PUFA fatty acids in their muscles.

The composition of these fatty acids therefor differs in wild herbivore muscle due to seasonal and regional variability of grasses. Palmitic (saturated), linoleic and γ-linolenic (polyunsaturated) acids are the major FA of grasses (Dungait, Docherty, Straker, & Evershed, 2010) while linoleic and λ- linolenic (and α-linolenic [ALA]) acids are essential FA as they are obtained solely from the diet. In addition, the high PUFA content has been associated with higher contraction frequencies of wild fowl and game animal muscles, compared to domestic cattle and chicken muscles (Valencak & Gamsjäger, 2014). The fatty acid profile is important when considering the health aspects of meat. A PUFA:SFA ratio of ≥ 0.45 and omega 6:omega 3 (n-6:n-3) of ≤ 4 is recommended for the meats consumed by humans (Warris, 2000) as a diet high in unsaturated FA provides health benefits. The meat from game animals generally adheres to this recommendation (Hoffman et al., 2010, Valencak & Gamsjäger, 2014, Valencak et al., 2015) and therefore appeals to the modern day consumer whom have become increasingly aware of the health attributes of game meat (MacMillan & Phillip, 2008). Although Quaresma et al. (2011) and Valencak et al. (2015) found a higher n-6:n-3 ratio in the meat of wild boar, it is still considered leaner compared to commercial pork meat, with a favourable PUFA:SFA ratio.

However, wild boar meat is considered as less desirable regarding aroma and flavour characteristics (Sales & Kotrba, 2013). There have been reports that the fresh meat from warthogs sometimes exhibits a flavour that is compared to boar taint. Boar taint is an undesirable odour and taste which may occur in the meat from entire male domestic pigs (*S. scrofa*), but has been associated with warthog meat from both genders and animals of different age classes. No research has been conducted of this particular aroma or flavour in the meat from warthogs or other wild suid species, and warrants further investigation to determine the potential influence it might have on consumers' willingness to buy and consume warthog meat products. Increased research efforts should aim to determine and characterize the physical, chemical and sensory parameters of the meat from wild animals.

The composition of IMF and fatty acids is primarily considered responsible for species-specific flavour of meat (Mottram, 1998), which is influenced by diet as mentioned. Consumers may alternately prefer the meat from grazing animals, associated with more intense aromas and flavours, or the meat from grain fed animals, associated with less intense aromas and flavours (Sañudo et al., 2000). Preference is also driven by consumers' unfamiliarity with flavours (Font-i-Furnols & Guerrero, 2014). Although all meat possess the desirable 'meaty' aroma and flavour, the sensory descriptors 'gamey' and 'livery' are the most suited to discriminate among the meat from different species as they differ significantly in intensity (Rødbotten et al., 2004). The meat from wild animals have more distinct gamey and livery flavours, while gamey flavour has been positively correlated with total fat and PUFA content in game meat (Hoffman et al., 2007b, Hoffman, Mostert, & Laubscher, 2009c). Daszkiewicz et al. (2015) found the meat from wild fallow deer had a higher total fat content, a more desirable fatty acid profile (increased PUFA content), higher aroma and flavour desirability and juiciness, compared to farmed fallow deer.

Fatty acids, iron content, and various volatile compounds have been implicated in metallic and livery flavour attributes of game meat. As PUFA oxidize more readily than SFA, meat high in total PUFA is more susceptible to lipid oxidation (Faustman et al., 2010) and the development of associated off-aromas and flavours which decreases meat quality and desirability. North and Hoffman (2015) found gamey flavour increased in springbok meat with ageing, which was attributed to increased lipid oxidation during the ageing period, while Mottram (1998) suggested that lipid oxidation occurs at slower rates during holding and storage than during cooking which may result in the formation of different volatile compounds. Developing processed game meat products is a potential strategy to introduce the meat of different game species to the commercial market, as the addition of preservatives and anti-oxidants, together with smoking and curing is used to inhibit and/or mask lipid and protein oxidation, thereby increasing shelf life and colour stability whilst imparting specific flavours (Banon, Costa, Gil, & Garrido, 2003, Gandemer, 2002). Considering the popularity of game meat products such as biltong in South Africa, and alheira sausages in Portugal, increasing research into game meat processing broadens the scope of wild animal production/consumption and global meat provision.

5 Value adding through meat processing

The growing human population places pressure on the agricultural industry to produce more food with the same resources, with hunger and malnutrition prevalent in developing countries (Bender, 1992).

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Meat is an important source of protein, vitamins and minerals (Lawrie & Ledward, 2006). Processing aims to preserve meat and its nutritional value, and simultaneously increase global supply and availability of meat (Decker & Park, 2010, Toldrá & Reig, 2011). Various meat products are processed from different muscles, muscle cuts and edible carcass offal, while certain muscle cuts, offal and "off-cuts" are not desired for whole or fresh consumption in some traditions. Processing therefore adds value to the meat production chain by increasing optimal utilization of the animal carcass, which results in higher profit rates for suppliers and processors (Kondaiah, 2004). Also, future trends in the meat industry is expected to encourage increased sustainable production and utilization of non-muscle based meat products (Kristensen et al., 2014).

Game meat has a reputation of being difficult to prepare, thus processed products that are convenient or ready-to-eat might have more appeal for consumers and further expand the market for game meat through value-adding (Hoffman, Muller, Schutte, & Crafford, 2004). Preservation processes such as curing, drying or fermentation aims to increase the shelf-life of meat products which makes them more readily available to consumers (Van Schalkwyk, McMillin, Booyse, Witthuhn, & Hoffman, 2011). However, processed meat products have a reputation of being unhealthy due to high fat content. For example, Soriano, Cruz, Gómez, Mariscal, and García Ruiz (2006) found commercial products made from deer (*C. elaphus*) meat was higher in fat content compared to the same products made from wild boar (*S. scrofa*), as producers added increased levels of fat to deer meat products because of the natural low fat content of deer meat. Most consumers show a preference for products with low amounts of visible fat, and are willing to pay more for these products if they are actually lower in fat as it is associated with increased quality (Girolami, Napolitano, Faraone, Di Bello, & Braghieri, 2014). Consumers also appreciate meat products that resemble traditional products in appearance and eating sensation (Tuorila, Meiselman, Cardello, & Lesher, 1998). The development of game meat products should therefore consider sensory, technological, safety and nutritional aspects of the product (Colmenero, 2000), while discerning consumers increasingly want a large variety of meat products that are healthy and of high quality (Issanchou, 1996, Kearney, 2010). Game meat, characterized by a lean profile, lends itself well as a substitute meat to reduce fat content of processed products, but not all products are suited for fat reduction strategies. Therefore, fat-reduced products should still satisfy consumers' expectations regarding distinctive visual qualities, display a level of familiarity, and with the added benefit of being healthier and organic (Grunert & Valli, 2001, Radder & le Roux, 2005), and not compromise on eating quality, safety and production costs (Colmenero, 2000, Grasso, Brunton, Lyng, Lalor, & Monahan, 2014).

Game meat has successfully been used in a variety of processed products with beneficial health benefits. For example, studies found that meat products produced from game meat in comparison with domestic animal meat have lower fat contents and higher nutritional values (Paleari, Moretti, Beretta, Mentasti,

& Bersani, 2003, Marino, Albenzio, della Malva, Muscio, & Sevi, 2015). However, Van Schalkwyk et al. (2011) found that game meat salami produced with springbok meat was inferior in terms of aroma and flavour compared to salami produced with the meat from other game animals, such as gemsbok, kudu and zebra.

As the meat from wild grazers is influenced by seasonal and regional variability of grasses, the products produced with game meat are likely to inherently vary in chemical composition and sensory aspects. Therefore, educating consumers on the quality attributes of game meat is necessary to encourage game meat and game meat products in general regarding acceptability and consumption. Also, as mentioned, the meat from wild animals is associated with a gamey or livery taste (Rødbotton et al., 2004), while game meat and the meat from non-ruminants is typically high in total unsaturated FA (UFA) content and thus more susceptible to lipid oxidation (Faustman et al., 2010), which leads to undesirable aromas and flavours. However, processes such as curing, smoking and addition of spices are used to inhibit the rate of oxidation and subsequent development of off-aromas and flavours, as well as imparting specific flavours (Gandemer, 2002). Nitrite as an anti-oxidant stabilizes the heme-iron group of the myoglobin molecule, chelates metal ions and radicals and reacts with UFA (Sebranek & Bacus, 2007), while certain phenolic compounds produced from wood-smoking scavenge oxygen radicals (Kjällstrand & Petersson, 2001). As noted by Sampels, Pickova, and Wiklund (2004), the chemical composition of smoked meat products depends on the smoking method used. For example, excessive dehydration may occur with hot smoking at temperatures of >60ºC (Fernandes et al., 2014), and lipolysis with drying at 40ºC (Sampels et al., 2004). Van Schalkwyk et al. (2011) found gamey flavour was not associated with cured smoked salami made from different game meats, and suggested that smoking reduces perceived game flavour in processed products, as the major quantity of volatile compounds may be derived from smoking in traditional smoked and cured products (Poligne, Collignan, & Trystram, 2002).

However, some of the polycyclic aromatic hydrocarbons (PAHs) derived from smoking comprise the largest class of carcinogenics (Šimko, 2002). A recent report (2015) by the WHO's International Agency for Research on Cancer (IARC) stated that the consumption of red meat and processed meat products is associated with the risk of certain types of cancer. The IARC placed processed products in the same category as asbestos, second-hand tobacco smoke and gamma radiation, claiming that consuming >50g of processed meat daily increases the risk of colorectal cancer by 18%. The study recommends reduced intake of red meat and processed products but acknowledged that meat is still a valuable source of high nutritional value (Bouvard et al., 2015). Therefore, future meat product development should aim to meet global health recommendations in terms of low total fat and SFA content, with favourable PUFA:SFA and n-6:n-3 ratios and decreased preservative content.

Apart from the association between the consumption of processed meat products and cancer, the traditional meat industry was also recently involved in meat adulteration and mislabelling scandals in Europe, South Africa, Mexico and Turkey. The substitution of horsemeat in traditional meat products negatively affected consumers' confidence in processed meat products and the meat supply chain in general, which reduced tendency to purchase processed products (Barnett et al., 2016). This resulted in consumer demand for improved regulation of and information on meat and meat products, along with concerns over safety and animal welfare. Although game meat is healthy, highly nutritious and can be produced safely and organically, Kane and Hellberg (2016) and Quinto, Tinoco, and Hellberg (2016) found that mislabelling of game meat products is higher compared to domestic or more familiar meat products. In order to improve confidence and purchase intention, Barnett et al. (2016) suggested to provide correct labelling on product ingredients, origin and traceability, shortening the meat sourcing and process chain, and improving regulation and communication. It follows that the future production and utilization of game meat depends on the ability of enterprises to standardize production and marketing strategies, and improve regulation and communication with consumers.

6 Warthogs as game meat

The meat production potential of the common warthog has been touched upon, with Crawford, Gale, and Woodford (1970) describing the muscle and adipose lipids of warthogs, Somers (1992) reporting on carcass yields in the Andries Vosloo Koedoe Reserve, Eastern Cape, and Hoffman and Sales (2007) investigating the physical and chemical characteristics of warthog meat. Similar to other game species, warthogs have a high dressing percentage, low total intramuscular lipid content, high total protein and moisture content and a favourable fatty acid (FA) profile. Traditionally considered as a popular bushmeat species they are hunted and utilized by local communities for subsistence, while local markets also trade in warthog ivory obtained from the tushes (formal term for tusks in this family). Although not considered as part of the formal game meat industry, Hoffman et al. (2005) found warthogs are a game meat species regularly consumed in South Africa and South African restaurants. The consumption of game meat is an important factor that promotes the social acceptability of hunting (Ljung et al., 2012), which is important since certain situations require the use of lethal methods for animal control, and for the existence of a lucrative safari hunting industry.

7 Conclusion

There is limited data available on the actual damages caused by warthogs and the associated ecological and economic implications, and this warrants further investigation as perceived and actual wildlife damage influences stakeholders' attitudes and responses towards wildlife. Although it is difficult to find a path of reconciliation between humans and damage causing species, Riley et al. (2003) notes the importance of integrating biological and human interests and increasing stakeholder involvement in wildlife management. Regardless of the potential disparities between perceived and actual wildlife damage, stakeholders' perceptions of wildlife damage influences their attitudes and responses towards wildlife and should be addressed in order to mediate conflicts.

The principles of wildlife management as documented for feral pigs provide a framework for the development and enforcement of relevant management strategies, while the science continues to grow and explore new avenues for applied management. Control strategies may only attempt to reduce population numbers or mitigate negative impacts experienced, but in certain situations wildlife and humans may find alternative ways to benefit from applied strategies, such as sustainable utilization of wildlife species. The potential of gaining profit from wildlife utilization has proved to serve as an incentive for South African farmers and land-owners to control wildlife and conserve areas of natural habitat. If the hunting of warthogs and subsequent processing of meat for commercial consumption can be facilitated, a commercial supply chain could be established that could benefit farmers and local communities and contribute towards local game meat production. Value adding through processing further expands the potential of game meat for the commercial market. People tend to be more positive towards wildlife despite associated damage if they are allowed to derive (consumptive) benefits from wildlife (Sifuna, 2010), which works towards sustainable management and tolerance of wildlife. Increased tolerance might work towards changing negative attitudes and encouraging sustainable utilization. It is suggested that research efforts should focus on bridging the gap between stakeholders' perceptions and management of wildlife in order to develop knowledge and understanding of wildlife dynamics.

8 References

Aaslyng, M. D., Bejerholm, C., Ertbjerg, P., Bertram, H. C., & Andersen, H. J. (2003). Cooking loss and juciness of pork in relation to raw meat quality and cooking procedure. *Food Quality and Preference*, *14*, 277–288.

Adams, C. R. (2000). Social acceptability's role in an expanded rational expectations model of intention to consume an innovative meat product in a restaurant setting. *Journal of Hospitality and Tourism Research*, *24*, 252–262. doi:10.1177/109634800002400208

Ali, R., & Pelkey, N. (2013). Satellite images indicate vegetation degradation due to invasive herbivores in the andaman islands. *Current Science*, *105*, 209–214.

Anonymous. (2006). Warthog preys on ostrich chicks. Retrieved November 11, 2015 from http://www.wilderness-safaris.com/blog/posts/warthog-preys-on-ostrich-chicks.

Anonymous. (2002, February). Making room for Mother Nature while protecting profits. *Hi Tech Security Solutions*. Retrieved from http://www.securitysa.com/5952N.

Arlet, M. E., & Molleman, F. (2007). Rodents damage crops more than wildlife in subsistence agriculture on the northern periphery of Dja Reserve, Cameroon. *International Journal of Pest Management*, *53*, 237–243. doi:10.1080/09670870701418994

Bailey, J. K., & Schweitzer, J. A. (2010). The role of plant resistance and tolerance to herbivory in mediating the effects of introduced herbivores. *Biological Invasions*, *12*, 337–351. doi:10.1007/s10530-009-9630-1

Ballari, S. A., & Barrios-García, M. N. (2014). A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. *Mammal Review*, *44*, 124–134. doi:10.1111/mam.12015

Ballari, S. A., Cuevas, M. F., Cirignoli, S., & Valenzuela, A. E. J. (2015). Invasive wild boar in Argentina: using protected areas as a research platform to determine distribution, impacts and management. *Biological Invasions*, *17*, 1595–1602. doi:10.1007/s10530-014-0818-7

Bamford, A. J., Ferrol-Schulte, D., & Wathan, J. (2014). Human and wildlife usage of a protected area buffer zone in an area of high immigration. *Oryx*, *48*, 504–513. doi:10.1017/S0030605313000215

Banon, S., Costa, E., Gil, M., & Garrido, M. (2003). A comparative study of boar taint in cooked and dry-cured meat. *Meat Science*, *63*, 381–388. Retrieved from http://www.sciencedirect.com/science/article/pii/S0309174002000979

Barnes, J. I., & de Jager, J. V. (1996). Economic and financial incentives for wildlife incentives on private land in Namibia and the implications for policy. *South African Journal of Wildlife Research*, *26*, 1–24.

Barnett, J., Begen, F., Howes, S., Regan, A., McConnon, A., Marcu, A., … Verbeke, W. (2016). Consumers' confidence, reflections and response strategies following the horsemeat incident. *Food Control*, *59*, 721–730. doi:10.1016/j.foodcont.2015.06.021

Barrio, I. C., Bueno, C. G., Villafuerte, R., & Tortosa, F. S. (2013). Rabbits, weeds and crops: Can agricultural intensification promote wildlife conflicts in semiarid agro-ecosystems? *Journal of Arid Environments*, *90*, 1–4. doi:10.1016/j.jaridenv.2012.10.016

Barrios-Garcia, M. N., & Ballari, S. A. (2012). Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biological Invasions*, *14*, 2283–2300. doi:10.1007/s10530-012-0229-6

Barrios-Garcia, M. N., & Simberloff, D. (2013). Linking the pattern to the mechanism: How an introduced mammal facilitates plant invasions. *Austral Ecology*, *38*, 884–890. doi:10.1111/aec.12027

Barron, M. C., Anderson, D. P., Parkes, J. P., & 'Ohukani'ohi'a Gon, S. M. III. (2011). Evaluation of feral pig control in Hawaiian protected areas using Bayesian catch-effort models. *New Zealand Journal of Zoology*, *35*, 182–188.

Bartoň, L., Bureš, D., Kotrba, R., & Sales, J. (2014). Comparison of meat quality between eland (*Taurotragus oryx*) and cattle (*Bos taurus*) raised under similar conditions. *Meat Science*, *96*, 346–52. doi:10.1016/j.meatsci.2013.07.016

Beck, A. (2008). *Electric fence induced mortality in South Africa*. MSc thesis, University of the Witwatersrand, Johannesburg, South Africa.

Begon, M., Townsend, C. R. & Harper, J. L. (2006). *Ecology: From Individuals to ecosystems* (4th Ed.). Oxford, England: Blackwell Publishing Ltd.

Bejerholm, C. & Aaslyng, M. D. (2004). Cooking of meat. In W. K. Jensen, D. Carrick, & M. Dikeman, M. (Eds.) *Encyclopedia of meat sciences* (pp. 343–349). Oxford, UK: Elsevier Ltd.

Bekker, J. L., Hoffman, L. C., & Jooste, P. J. (2012). Wildlife-associated zoonotic diseases in some southern African countries in relation to game meat safety: a review. *The Onderstepoort Journal of Veterinary Research*, *79*(1), E1–E12. doi:10.4102/ojvr.v79i1.422

Bender A. (1992). Meat and meat products in human nutrition in developing countries. FAO and INPhO, Food and Nutrition Paper 53. Rome, Italy: Food and Agriculture Organization of the United Nations. Retrieved from http://www.fao.org/docrep/t0562e/t0562e00.HTM.

Bengsen, A. J., Gentle, M. N., Mitchell, J. L., Pearson, H. E., & Saunders, G. R. (2014). Impacts and management of wild pigs *Sus scrofa* in Australia. *Mammal Review*, *44*, 135–147. doi:10.1111/mam.12011

Bengsen, A. J., Leung, L. K. P., Lapidge, S. J., & Gordon, I. J. (2010). Artificial illumination reduces bait-take by small rainforest mammals. *Applied Animal Behaviour Science*, *127*, 66–72. doi:10.1016/j.applanim.2010.08.006

Benson, D. E. (1991). Values and management of wildlife and recreation on private land in South Africa. *Wildlife Society Bulletin*, *19*, 497–510.

Bernard, R. T. F., & Parker, D. M. (2006). The use of archaeological and ethnographical information to supplement the historical record of the distribution of large mammalian herbivores in South Africa. *South African Journal of Science*, *102*, 117–119.

Bhola, N., Ogutu, J. O., Piepho, H. P., Said, M. Y., Reid, R. S., Hobbs, N. T., & Olff, H. (2012). Comparative changes in density and demography of large herbivores in the Masai Mara Reserve and its surrounding human-dominated pastoral ranches in Kenya. *Biodiversity and Conservation*, *21*, 1509–1530. doi:10.1007/s10531-012-0261-y

Bieber, C., & Ruf, T. (2005). Population dynamics in wild boar *Sus scrofa*: Ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *Journal of Applied Ecology*, *42*, 1203–1213. doi:10.1111/j.1365-2664.2005.01094.x

Biedrzycka, A., Solarz, W., & Okarma, H. (2012). Hybridization between native and introduced species of deer in Eastern Europe, *93*, 1331–1341. doi:10.1644/1

Boast, L. K., & Houser, A. M. (2008). *Large predator spoor survey on Game and Cattle farmland in Ghanzi, Botswana*. Unpublished research report, Cheetah Conservation Botswana. Retrieved

Stellenbosch University http://scholar.sun.ac.za

from http://www.guidetrainingcourses.com/wp-content/uploads/2013/10/Large-predator-spoor-survey-on-Game-and-Cattle-farmland-in-Ghanzi-Botswana-July-2008.pdf

Boeken, B., Shachak, M., Gutterman, Y., & Brand, S. (1995). Patchiness and disturbance: Plant community responses to porcupine diggings in the central Negev. *Ecography*, *18*, 410–422. doi:10.1111/j.1600-0587.1995.tb00144.x

Bomford, M., & O'Brien, P. (1995). Eradication or control for vertebrate pests? *Wildlife Society Bulletin*, *23*, 249–255. Retrieved from http://www.jstor.org/stable/3782799

Bond, W., & Loffell, D. (2001). Introduction of giraffe changes acacia distribution in a South African savanna. *African Journal of Ecology*, *39*, 286–294. Retrieved from http://onlinelibrary.wiley.com/doi/10.1046/j.1365-2028.2001.00319.x/full

Bonnington, C., Grainger, M., Dangerfield, S., & Fanning, E. (2009). The influence of electric fences on large mammal movements in the Kilombero Valley, Tanzania. *African Journal of Ecology*, *48*, 280–284.

Boshe, J. I. (1981). Reproductive ecology of the warthog *Phacochoerus aethiopicus* and its significant fot management in the eastern Selous Game Reserve, Tanzania. *Biological Conservation*, *20*, 37–44.

Boshoff, A. F., & Kerley, G. I. H. (2013). *Historical incidence of the larger mammals in the Free State province (South Africa) and Lesotho*. Port Elizabeth, South Africa: Centre for African Conservation Ecology, Nelson Mandela Metropolitan University.

Boshoff, A. F., & Kerley, G. I. H. (2001). Potential distributions of the medium- to large-sized mammals in the Cape Floristic Region, based on historical accounts and habitat requirements. *African Zoology*, *36*, 245–273.

Boshoff, A., Landman, M., & Kerley, G. (2015). Filling the gaps on the maps : historical distribution patterns of some larger mammals in part of southern Africa. *Transactions of the Royal Society of South Africa*. doi:10.1080/0035919X.2015.1084066

Botha, M. S., & Stock, W. D. (2005). Stable isotope composition of faeces as an indicator of seasonal diet selection in wild herbivores in southern Africa. *South African Journal of Science*, *101*, 371–374.

Bouton, P. E., Harris, P. V, & Shorthose, W. R. (1971). Effect of ultimate pH upon the water-holding capacity and tenderness of mutton. *Journal of Food Science*, *36*, 435–439.

Bouvard, V., Loomis, D., Guyton, K. Z., Grosse, Y., El Ghissassi, F., Benbrahim-Tallaa, .L,…& Straif, K. (2015). Carcinogenicity of consumption of red and processed meat. *The Lancet Oncology*. doi.org/10.1016/S1470-2045(15)00444-1.

Bracke, M. B. M. (2011). Review of wallowing in pigs: Description of the behaviour and its motivational basis. *Applied Animal Behaviour Science*, *132*, 1–13. doi:10.1016/j.applanim.2011.01.002

Bradley, R. M. (1971). Warthog (*Phacochoerus aethiopicus* Pallas) burrows in Nairobi National Park. *East African Journal of Ecology, 9*, 149-151.

Braga, C., Alexandre, N., Fernández-Llario, P., & Santos, P. (2010). Wild boar (*Sus scrofa*) harvesting using the espera hunting method: side effects and management implications. *European Journal of Wildlife Research*, *56*, 465–469. doi:10.1007/s10344-010-0373-1

Bragg, C. J., Donaldson, J. D., & Ryan, P. G. (2005). Density of Cape porcupines in a semi-arid environment and their impact on soil turnover and related ecosystem processes. *Journal of Arid Environments*, *61*, 261–275. doi:10.1016/j.jaridenv.2004.09.007

Bryden, H. A. (1893). *Gun and camera in Southern Africa*. *Edward Stanford*. London: Edward Stanford. Retrieved from https://archive.org/details/guncamerainsouth00bryd

Bueno, C. G., Barrio, I. C., García-González, R., Alados, C. L., & Gómez-García, D. (2010). Does wild boar rooting affect livestock grazing areas in alpine grasslands? *European Journal of Wildlife Research*, *56*, 765–770. doi:10.1007/s10344-010-0372-2

Bueno, C. G., Reiné, R., Alados, C. L., & Gómez-García, D. (2011). Effects of large wild boar disturbances on alpine soil seed banks. *Basic and Applied Ecology*, *12*, 125–133. doi:10.1016/j.baae.2010.12.006

Burchell, W. J. (1822, 1823). *Travels in the interior of Southern Africa (Vol 1 & 2)*. London, England. Longmans, Hurst, Rees, Orme, Brown and Green.

Burger, J. (2002). Daily consumption of wild fish and game: exposures of high end recreationists. *International Journal of Environmental Health Research*, *12*, 343–54. doi:10.1080/0960312021000056393

Busby, P., Vitousek, P., & Dirzo, R. (2010). Prevalence of tree regeneration by sprouting and seeding along a rainfall gradient in Hawai'i. *Biotropica*, *42*, 80–86. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.1744-7429.2009.00540.x/full

Cai, J., Jiang, Z., Zeng, Y., Li, C., & Bravery, B. D. (2008). Factors affecting crop damage by wild boar and methods of mitigation in a giant panda reserve. *European Journal of Wildlife Research*, *54*, 723–728. doi:10.1007/s10344-008-0203-x

Calenge, C., Maillard, D., Fournier, P., & Fouque, C. (2004). Efficiency of spreading maize in the garrigues to reduce wild boar (*Sus scrofa*) damage to Mediterranean vineyards. *European Journal of Wildlife Research*, *50*, 112–120. doi:10.1007/s10344-004-0047-y

Calvino-Cancela, M. (2011). Seed dispersal of alien and native plants by vertebrate herbivores. *Biological Invasions*, *13*, 895–904. doi:10.1007/s10530-010-9877-6

Campbell, T. A., Long, D. B., Lavelle, M. J., Leland, B. R., Blankenship, T. L., & Vercauteren, K. C. (2012). Impact of baiting on feral swine behavior in the presence of culling activities. *Preventive Veterinary Medicine*, *104*, 249–57. doi:10.1016/j.prevetmed.2012.01.001

Campos, C. M., Peco, B., Campos, V. E., Malo, J. E., Giannoni, S. M., & Suárez, F. (2008). Endozoochory by native and exotic herbivores in dry areas: consequences for germination and survival of *Prosopis* seeds. *Seed Science Research*, *18*, 91–100. doi:10.1017/S0960258508940344

Caro, T. M. (2005). Behavioural indicators of exploitation. *Ethology Ecology & Evolution*, *17*, 189–194. doi:10.1080/08927014.2005.9522608

Carpio, A. J., Guerrero-Casado, J., Tortosa, F. S., & Vicente, J. (2014). Predation of simulated red-legged partridge nests in big game estates from South Central Spain. *European Journal of Wildlife Research*, *60*, 391–394. doi:10.1007/s10344-013-0786-8

Carruthers, J. (2005). " Wilding the farm or farming the wild "? The evolution of scientific game ranching in South Africa from the 1960s to the present. *Transactions of the Royal Society of South Africa*, *63*, 160–181.

Castley, J. G., Boshoff, A. F., & Kerley, G. I. H. (2001). Compromising South Africa's natural biodiversity - inappropriate herbivore introductions. *South African Journal of Science*, *97*, 344–348.

Chaminuka, P., Udo, H. M. J., Eilers, K. C. H. A. M., & van der Zijpp, A. (2014). Livelihood roles of cattle and prospects for alternative land uses at the wildlife / livestock interface in South Africa. *Land Use Policy*, *38*, 80–90. doi:10.1016/j.landusepol.2013.10.007

Chaudhry, M. J. I., Ogada, D. L., Malik, R. N., Virani, M. Z., & Giovanni, M. D. (2012). First evidence that populations of the critically endangered Long-billed Vulture *Gyps indicus* in Pakistan have increased following the ban of the toxic veterinary drug diclofenac in south Asia. *Bird Conservation International*, *22*, 389–397. doi:10.1017/S0959270912000445

Chevallier, N., & Ashton, B. (2006). *A report on the Porcupine quill trade in South Africa*. Retrieved November 8, 2015 from http://media.withtank.com/23fd88d381/porcupine_quill_trade.pdf

Child, B. A., Musengezi, J., Parent, G. D., & Child, G. F. T. (2012). The economics and institutional economics of wildlife on private land in Africa. *Pastoralism: Research, Policy and Practice*, *2*, 18. doi:10.1186/2041-7136-2-18

Child, G., Roth, H. H. & Kerr, M. (1968). Reproduction and recruitment patterns in warthog *(Phacochoerus aethiopicus)* populations. *Mammalia, 32*, 6-29.

Child, M. F., Raimondo, D., Do Linh San, E., Roxburgh L., & Davies-Mostert, H. (in press.). *The Red List of Mammals of South Africa, Swaziland and Lesotho*. Pretoria, South Africa: South African National Biodiversity Institute and Endangered Wildlife Trust.

Choe, J. H., Choi, Y. M., Lee, S. H., Shin, H. G., Ryu, Y. C., Hong, K. C., & Kim, B. C. (2008). The relation between glycogen, lactate content and muscle fiber type composition, and their influence on postmortem glycolytic rate and pork quality. *Meat Science*, *80*, 355–362. doi:10.1016/j.meatsci.2007.12.019

Chomba, C. (2012). Patterns of human wildlife conflicts in Zambia, causes, consequences and management responses. *Journal of Ecology and The Natural Environment*, *4*, 303–313. doi:10.5897/JENE12.029

Choquenot, D., Kilgour, R., & Lukins, B. (1993). An evaluation of feral pig trapping. *Wildlife Research*, *20*, 15. doi:10.1071/WR9930015

Choquenot, D., Lukins, B., & Curran, G. (1997). Assessing lamb predation by feral pigs in Australia's semi-arid rangelands. *Journal Applied Ecology*, *34*, 1445–1454.

Chown, S. L., Spear, D., Lee, J. E., & Shaw, J. D. (2009). Animal introductions to southern systems: lessons for ecology and policy. *African Zoology*, *44*, 248–262.

Clauss, M., Nijboer, J., Loermans, J. H. M., Roth, T., Van Der Kuilen, J., & Beynen, A. C. (2008). Comparative digestion studies in wild suids at Rotterdam Zoo. *Zoo Biology*, *27*, 305–319. doi:10.1002/zoo.20191

Clevenger, A. P., Chruszcz, B., Gunson, K. E., Gunson, K. F., & Clevenger, P. (2014). Highway mitigation fencing reduces wildlife-vehicle collisions. *Wildlife Society Bulletin*, *29*, 646–653.

Clough, G. (1969). Some preliminary observations on reproduction in the warthog, *Pharcochoerus aethiopicus* Pallas. *Journal of Reproduction and Fertility, 6*, 323–337.

Clout, M., & Russell, J. (2007). The invasion ecology of mammals: a global perspective. *Wildlife Research*, *35*, 180–184. Retrieved from http://www.publish.csiro.au/paper/WR07091

Codron, D., & Codron, J. (2009). Reliability of 13C and 15N in faeces for reconstructing savanna herbivore diet. *Mammalian Biology*, *74*, 36–48. doi:10.1016/j.mambio.2007.12.005

Codron, D., Codron, J., Lee-Thorp, J. A., Sponheimer, M., de Ruiter, D., Sealy, J., … Fourie, N. (2007a). Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology*, *273*, 21–29. doi:10.1111/j.1469-7998.2007.00292.x

Codron, D., Lee-Thorp, J. A., Sponheimer, M., Codron, J., De Ruiter, D., & Brink, J. S. (2007b). Significance of diet type and diet quality for ecological diversity of African ungulates. *Journal of Animal Ecology*, *76*, 526–537. doi:10.1111/j.1365-2656.2007.01222.x

Coe, M. J., & Skinner, J. D. (1993). Connections, disjunctions and endemism in the eastern and southern African mammal faunas. *Transaction of Royal Society of South Africa, 48*, 233-255.

Coetsee, C., Stock, W. D., & Craine, J. M. (2010). Do grazers alter nitrogen dynamics on grazing lawns in a South African savannah ? *African Journal of Zoology*, *49*, 62–69.

Colautti, R. I., Ricciardi, A., Grigorovich, I. A., & MacIsaac, H. J. (2004). Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, *7*, 721–733. doi:10.1111/j.1461-0248.2004.00616.x

Colmenero, F. J. (2000). Relevant factors in strategies for fat reduction in meat products. *Trends in Food Science & Technology*, *11*, 56–66. Retrieved from http://www.sciencedirect.com/science/article/pii/S092422440000042X

Conover, M. R. (1994). Perceptions of the grass-roots leaders of the agricultural community about wildlife damage on their farms and ranches. *Wildlife Society Bulletin*, *22*, 94–100.

Conover, M. R. (1998). Perceptions of American agricultural producers about wildlife on their farms and ranches. *Wildlife Society Bulletin*, *26*, 597–604.

Conover, M. R., Pitt, W. C., Kessler, K. K., DuBow, T. J., & Sanborn, W. A. (1995). Review of human injuries, illnesses, and economic losses caused by wildlife in the United States. *Wildlife Society Bulletin*, *23*, 407–414. Retrieved from http://www.jstor.org/stable/3782947

Constible, J. M., Sweitzer, R. A., Van Vuren, D. H., Schuyler, P. T., & Knapp, D. A. (2005). Dispersal of non-native plants by introduced bison in an island ecosystem. *Biological Invasions*, *7*, 699–709. doi:10.1007/s10530-004-5859-x

Cooke, H. B. S. (1949). Fossil mammals of the Vaal River deposits. *Geological Survey of South Africa Memoir, 35*, 1–109.

Cousins, J. A., Sadler, J. P., & Evans, J. (2010). The challenge of regulating private wildlife ranches for conservation in South Africa. *Ecology and Society*, *15,* 28. Retrieved from http://www.ecologyandsociety.org/vol15/iss2/art28/

Craig, T. P. (2010). The resource regulation hypothesis and positive feedback loops in plant – herbivore interactions. *Population Ecology*, *52*, 461–473. doi:10.1007/s10144-010-0210-0

Crawford, M. A, Gale, M. M., & Woodford, M. H. (1970). Muscle and adipose tissue lipids of warthog, *Phacochoerus aethiopicus*. *International Journal of Biochemistry*, *1*, 654–658. doi:10.1016/0020-711x(70)90039-x

Cromsigt, J. P. G. M., & Olff, H. (2006). Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. *Ecology*, *87*, 1532–1541. Retrieved from http://www.esajournals.org/doi/abs/10.1890/0012-9658(2006)87%5B1532:RPASGM%5D2.0.CO%3B2

Cromsigt, J. P. G. M., Kuijper, D. P. J., Adam, M., Beschta, R. L., Churski, M., Eycott, A., … West, K. (2013). Hunting for fear: innovating management of human-wildlife conflicts. *Journal of Applied Ecology*, *50*, 544–549. doi:10.1111/1365-2664.12076

Cuevas, M. F., Mastrantonio, L., Ojeda, R. A., & Jaksic, F. M. (2012). Effects of wild boar disturbance on vegetation and soil properties in the Monte Desert, Argentina. *Mammalian Biology - Zeitschrift Für Säugetierkunde*, *77*, 299–306. doi:10.1016/j.mambio.2012.02.003

Cuevas, M. F., Ojeda, R. A., Dacar, M. A., & Jaksic, F. M. (2013). Seasonal variation in feeding habits and diet selection by wild boars in a semi-arid environment of Argentina. *Acta Theriologica*, *58*, 63–72. doi:10.1007/s13364-012-0105-x

Cumming, D. H. M. (1999). *Study on the development of Transboundary Natural Resource Management areas in southern Africa-Environmental Context: Natural Resource, Land Use, and Conservation*. Washington, DC, USA: Biodiversity Support Program.

Cumming, D. H. M. (2008). *Phacochoerus africanus, Common Warthog*. *The IUCN Red List of Threatened Species*. Retrieved from http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T41768A10535705.en

D'Huart, J. P., Nowak-Kemp, P. M., & Butynski, T. M. (2013). A seventeenth-century warthog skull in Oxford, England. *Archives of natural history, 40*, 294-301.

D'Huart, J.-P., & Grubb, P. (2001). Distribution of the common warthog (*Phacochoerus africanus*) and the desert warthog (*Phacochoerus aethiopicus*) in the Horn of Africa. *African Journal of Ecology*, *39*, 156–169. doi:10.1046/j.0141-6707.2000.00298.x

Dai, F., Feng, D., Cao, Q., Ye, H., Zhang, C., & Xia, W. (2009). Developmental differences in carcass, meat quality and muscle fibre characteristics between the Landrace and a Chinese native pig. *South African Journal of Animal Sciences*, *39*, 267–273.

Dannenberger, D., Nuernberg, G., Nuernberg, K., & Hagemann, E. (2013). The effects of gender, age and region on macro- and micronutrient contents and fatty acid profiles in the muscles of roe deer and wild boar in Mecklenburg-Western Pomerania (Germany). *Meat Science*, *94*, 39–46. doi:10.1016/j.meatsci.2012.12.010

Daszkiewicz, T., Hnatyk, N., Dąbrowski, D., Janiszewski, P., Gugołek, A., Kubiak, D., … Koba-Kowalczyk, M. (2015). A comparison of the quality of the *Longissimus lumborum* muscle from wild and farm-raised fallow deer (*Dama dama* L.). *Small Ruminant Research*, *129*, 77–83. doi:10.1016/j.smallrumres.2015.05.003

Daszkiewicz, T., Janiszewski, P., & Wajda, S. (2009). Quality characteristics of meat from wild red deer (*Cervus elaphus* L.) hinds and stags. *Journal of Muscle Foods*, *20*, 428–448.

Daszkiewicz, T., Kubiak, D., Winarski, R., & Koba-Kowalczyk, M. (2012). The effect of gender on the quality of roe deer (*Capreolus capreolus* L.) meat. *Small Ruminant Research*, *103*, 169–175. doi:10.1016/j.smallrumres.2011.09.044

Davis, N. E., Forsyth, D. M., & Coulson, G. (2010). Facilitative interactions between an exotic mammal and native and exotic plants: hog deer (*Axis porcinus*) as seed dispersers in south-eastern Australia. *Biological Invasions*, *12*, 1079–1092. doi:10.1007/s10530-009-9525-1

Day, T., & Macgibbon, R. (2007). Multiple-species exclusion fencing and technology for mainland sites. In G. W. Witmer, W. C. Pitt, & K. A. Fagerstone (Eds.), *Managing Vertebrate Invasive Species: Proceedings of an International Symposium* (pp. 418–433). Fort Collins, CO.

De Jong, Y. A., Culverwell, J., & Butynski, T. M. (2009). Desert warthog found in Tsavo East National Park and Tsavo West National Park. *Suiform Soundings*, *8*, 11–12.

De Villiers, M., & Van Aarde, R. (1994). Aspects of habitat disturbance by Cape porcupines in a savanna ecosystem. *South African Journal of Zoology*, *29*, 217–220. Retrieved from http://www.ceru.up.ac.za/downloads/Aspects_habitat_porcupines.pdf

De Wet, P. (2010). Predation Management Forum: Norms and Standards for the management of damage-causing animals in South Africa. In M. Jackson (Chair), *Meeting of the Parliamentary Monitoring Group*, Cape Town, South Africa. Retrieved from http://www.pmg.org.za/report/20101102-norms-and-standards-management-damage-causing-animals-south-africa.

Dean, W. R. J., & Milton, S. J. (1991). Disturbances in semi-arid shrubland arid grassland in the Karoo, South Africa: mammal diggings as germination sites. *African Journal of Ecology*, *29*, 11–16. doi:10.1111/j.1365-2028.1991.tb00815.x

Decker, E. A., & Park, Y. (2010). Healthier meat products as functional foods. *Meat Science*, *86*, 49–55. doi:10.1016/j.meatsci.2010.04.021

Department of Agriculture, Forestry and Fisheries (DAFF). (2013a). *South African Yearbook 2012/13: Agriculture, Forestry and Fisheries*. In A. Vermeulen (Ed.) (pp 44–82). Pretoria, South Africa: Department of Agriculture, Forestry and Fisheries. Retrieved from http://www.gcis.gov.za.

Department of Agriculture, Forestry and Fisheries (DAFF). (2013b). *Abstract of Agricultural Statistics 2013.* Compiled by Directorate Statistics and Economic Analysis. Pretoria, South Africa: Department of Agriculture, Forestry and Fisheries. Retrieved from www.nda.agric.za

Department of Environmental Affairs (DEA). (2010). National Environmental Management: Biodiversity Act 2004 (Act No. 10 of 2004). Draft norms and standards for management of damage-causing animals in South Africa. Government Gazette (33806). Retrieved from https://www.environment.gov.za/sites/default/files/gazetted_notices/nemba_draftnormsandstandards_g33806gen1084.pdf

Department of Environmental Affairs (DEA). (2014). National Environmental Management: Biodiversity Act 2004 (Act No. 10 of 2004): Alien and Invasive Species Regulations. Government Gazette (36683). doi:http://dx.doi.org/9771682584003-32963

Department of Environmental Affairs (DEA). (2015). National Environmental Management: Biodiversity Act, 2004 (Act No. 10 of 2004). *Norms and standards for the translocation of indigenous species in South Africa. Volume 595, Government Gazette (38395).* Pages 1–16. Government Printer: Pretoria, South Africa. Retrieved from www.gpwinline.co.za. doi:http://dx.doi.org/9771682584003-32963.

Department of Transport (DAT). (2011). *Road Traffic Report 31 March 2011*. Road Traffic Management Corporation. Retrieved from https://www.arrivealive.co.za/documents/March%202011%20Road%20Traffic%20Report.pdf

Desbiez, A. L., Keuroghlian, A., Piovezan, U., & Bodmer, R. E. (2011). Invasive species and bushmeat hunting contributing to wildlife conservation: the case of feral pigs in a Neotropical wetland. *Oryx*, *45*, 78–83. doi:10.1017/S0030605310001304

DeVault, T. L., & Rhodes, O. E. (2002). Identification of vertebrate scavengers of small mammal carcasses in a forested landscape. *Acta Theriologica*, *47*, 185–192. doi:10.1007/BF03192458

Dolbeer, R. A. (1998). Population dynamics: Age foundation of wildlife damage management for the 21st century. In *Vertebrate Pest Conference Proceedings* (pp. 1–11). Costa Mesa.

Dovrat, G., Perevolotsky, A., & Ne'eman, G. (2012). Wild boars as seed dispersal agents of exotic plants from agricultural lands to conservation areas. *Journal of Arid Environments*, *78*, 49–54. doi:10.1016/j.jaridenv.2011.11.011

Dreyer, T. F, & Lyle, A. (1931). *New fossil mammals and man from South Africa*. Bloemfontein, South Africa: Nasionale Pers.

Dry, G. (2010). Commercial wildlife ranching's contribution to the green economy. Retrieved from http://www.sawma.co.za/images/Dry_Gert_Full_paper.pdf.

Dry, G. (2012, Spring). Die gesig van groen. *Wildlife Ranching South Africa (WRSA)*, p. 15–19. Retrieved from http://www.wrsa.co.za/wrsa-e-magazine/book/3-spring-2012-publication/2-wrsa-publications.

Du Toit, J. & Cumming, D. (1999). Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity & Conservation*, 1643–1661. Retrieved from http://link.springer.com/article/10.1023/A:1008959721342

Dungait, J. A., Docherty, G., Straker, V., & Evershed, R. P. (2010). Seasonal variations in bulk tissue, fatty acid and monosaccharide delta(13)C values of leaves from mesotrophic grassland plant communities under different grazing managements. *Phytochemistry*, *71*, 415–28. doi:10.1016/j.phytochem.2009.10.010

Elledge, A. E., McAlpine, C. A., Murray, P. J., & Gordon, I. J. (2012). Modelling habitat preferences of feral pigs for rooting in lowland rainforest. *Biological Invasions*, *15*, 1523–1535. doi:10.1007/s10530-012-0387-6

Ellerman, J. R., Morrison-Scott, T. C. S., & Hayman, R. W. (1953). *South African Mammals 1758 to 1951: A reclassification.* London, England: The Trustees of the British Museum.

Eloff, P. J., & Niekerk, A. Van. (2005). Game , fences and motor vehicle accidents : spatial patterns in the Eastern Cape. *South African Journal of Wildlife Research*, *35*, 125–130.

Elsey, R. M., Mouton, E. C., & Kinler, N. (2012). Effects of feral swine (*Sus scrofa*) on alligator (*Alligator mississippiensis*) nests in Louisiana. *Southeastern Naturalist*, *11*, 205–218. doi:10.1656/058.011.0204

Engeman, R., Hershberger, T., Orzell, S., Felix, R., Killian, G., Woolard, J., … Avery, M. (2014). Impacts from control operations on a recreationally hunted feral swine population at a large military installation in Florida. *Environmental Science and Pollution Research International*, *21*, 7689–97. doi:10.1007/s11356-014-2727-9

England, E. M., Matarneh, S. K., Scheffler, T. L., Wachet, C., & Gerrard, D. E. (2014). pH inactivation of phosphofructokinase arrests postmortem glycolysis. *Meat Science*, *98*, 850–7. doi:10.1016/j.meatsci.2014.07.019

Enser, M., Hallett, K., Hewitt, B., Fursey, G. A. J., & Wood, J. D. (1996). Fatty acid content and composition of English beef, lamb and pork at retail. *Meat Science*, *42*, 443–456. doi:10.1016/0309-1740(95)00037-2

Ewer, R. F. (1957). A collection of *Phacochoerus aethiopicus* teeth from the Kalkbank Middle Stone Age Site, Central Transvaal. *Paleontology Africana*, *5*, 5-20.

Farouk, M. M., Beggan, M., Hurst, S., Stuart, A., Dobbie, P. M., & Bekhit, A. E. D. (2007). Meat quality attributes of chilled venison and beef. *Journal of Food Qulity*, *30*, 1023–1039.

Faustman, C., Sun, Q., Mancini, R., & Suman, S. P. (2010). Myoglobin and lipid oxidation interactions : Mechanistic bases and control. *Meat Science*, *86*, 86–94. doi:10.1016/j.meatsci.2010.04.025

Fenta, M. M. (2014). Human-wildlife conflicts: Case study in Wondo Genet District, Southern Ethiopia. *Agriculture, Forestry and Fisheries*, 3, 352–362. doi:10.11648/j.aff.20140305.14

Fernandes, V. R. T., Souza Franco, M. L. R., Mikcha, J. M. G., de Souza, V. L. F., Gasparino, E., Coutinho, M. E., … Del Vesco, A. P. (2014). Yacare caiman (Caiman yacare) trim hamburger and sausage subjected to different smoking techniques. *Journal of the Science of Food and Agriculture*, *94*, 468–72. doi:10.1002/jsfa.6270

Ferreira, S., Gaylard, A., Greaver, C., Hayes, J., Cowell, C., & Ellis, G. (2010). *Annual Report 2011/2012. South African National Parks*. Retrived from https://www.sanparks.org/assets/docs/general/annual-report-2012.pdf.

Festa–Bianchet, M. (2008). Ecology, evolution, economics, and ungulate management. In T. E. Fulbright, & D. G. Hewitt (Eds.), *Wildlife science: Linking ecological theory and management applications* (pp. 183–202). Florida, USA: CRC, Boca Raton.

Field, C. R. (1970). Observations on the food habits of tame warthog and antelope in Uganda. *East African Wildlife Journal*, *8*, 1–17.

Fincham, J. E., & Hobbs, J. A. (2013). Feral pigs: A threat to ground-nesting birds. *Ornithological Observations*, *4*, 83–89.

Focardi, S., Capizzi, D., & Monetti, D. (2000). Competition for acorns among wild boar (*Sus scrofa*) and small mammals in a Mediterranean woodland. *Journal of Zoology*, *250*, 329–334. Retrieved from http://journals.cambridge.org/abstract_S095283690000306X

Font-i-Furnols, M., & Guerrero, L. (2014). Consumer preference, behavior and perception about meat and meat products: An overview. *Meat Science*, *98*, 361–71. doi:10.1016/j.meatsci.2014.06.025

Forsyth, D. M., & Duncan, R. P. (2001). Propagule size and the relative success of exotic ungulate and bird introductions to New Zealand. *The American Naturalist*, *157*, 583–95. doi:10.1086/320626

Forsyth, D. M., Duncan, R. P., Bomford, M., & Moore, G. (2004). Climatic suitability, life-history traits, introduction effort, and the establishment and spread of introduced mammals in Australia. *Conservation Biology*, *18*, 557–569. doi:10.1111/j.1523-1739.2004.00423.x

Frackowiak, W., Gorczyca, S., Merta, D., & Wojciuch-Ploskonka, M. (2013). Factors affecting the level of damage by wild boar in farmland in north-eastern Poland. *Pest Management Science*, *69*, 362–366. doi:10.1002/ps.3368

Fraser, K. W., Cone, J. M., & Whitford, E. J. (2000). A revision of the established ranges and new populations of 11 introduced ungulate species in New Zealand. *Journal of the Royal Society of New Zealand*, *30*, 419–437. doi:10.1080/03014223.2000.9517633

Frederick, J. M. (1998). Overview of wild pig damage in California. In R. O. Baker & A. C. Crabb (Eds.), *Proceedings 18th Vertebrate Pest Conference* (pp. 82–86). Davis, USA: University of California.

Fuhlendorf, S. D., & Smeins, F. E. (1999). Scaling effects of grazing in a semi-arid grassland. *Journal of Vegetation Science*, *10*, 731–738.

Gamelon, M., Besnard, A., & Gaillard, J. (2011). High hunting pressure selects for earlier birth date: wild boar as a case study. *Evolution, 65*, 3100–3112. doi: 10.1111/j.1558-5646.2011.01366

Gamelon, M., Gaillard, J.-M., Servanty, S., Gimenez, O., Toïgo, C., Baubet, E., … Lebreton, J.-D. (2012). Making use of harvest information to examine alternative management scenarios: a body weight-structured model for wild boar. *Journal of Applied Ecology*, *49*, 833–841. doi:10.1111/j.1365-2664.2012.02160.x

Gandemer, G. (2002). Lipids in muscles and adipose tissues, changes during processing and sensory properties of meat products. *Meat Science*, *62*, 309–321. doi:10.1016/S0309-1740(02)00128-6

Geisser, H., & Reyer, H. (2004). Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. *The Journal of Wildlife Management*, *68*, 939–946.

Gentle, M., Speed, J., & Pople, A. (2014). Impacts on nontarget avian species from aerial meat baiting for feral pigs. *Ecological Management & Restoration*, *15*, 222–230. doi:10.1111/emr.12132

Gillingham, S., & Lee, P. C. (2003). People and protected areas: a study of local perceptions of wildlife crop-damage conflict in an area bordering the Selous Game Reserve, Tanzania. *Oryx*, *37*, 316–325. doi:10.1017/S0030605303000577

Girolami, A., Napolitano, F., Faraone, D., Di Bello, G., & Braghieri, A. (2014). Image analysis with the computer vision system and the consumer test in evaluating the appearance of Lucanian dry sausage. *Meat Science*, *96*, 610–6. doi:10.1016/j.meatsci.2013.08.006

Golden, K. E., Peterson, M. N., De Perno, C. S., Bardon, R. E., & Moorman, C. E. (2013). Factors shaping private landowner engagement in wildlife management. *Wildlife Society Bulletin*, *37*, 94–100. doi:10.1002/wsb.235

Grasso, S., Brunton, N. P., Lyng, J. G., Lalor, F., & Monahan, F. J. (2014). Healthy processed meat products – Regulatory, reformulation and consumer challenges. *Trends in Food Science & Technology*, *39*, 4–17. doi:10.1016/j.tifs.2014.06.006

Grubb, P. & Oliver, W. (1991). A forgotten warthog. *Species, 17*, 61.

Grubb, P., & D'Huart, J. (2010). Rediscovery of the Cape warthog *Phacochoerus aethiopicus*: a review. *Journal of East African Natural History*, *99*, 77–102. Retrieved from http://www.bioone.org/doi/abs/10.2982/028.099.0204

Grubb, P., Sandrock, O., Kullmer, O., Kaiser, T. M., & Schrenk, F. (1999). Relationships between eastern and southern African mammal faunas. In T. G. Bromage, & F. Schrenk (Eds.), *African biogeography, climate change and human evolution* (pp. 253–267). Oxford, UK: Oxford University Press.

Grunert, K. G., & Valli, C. (2001). Designer-made meat and dairy products: consumer-led product development. *Livestock Production Science*, *72*, 83–98. doi:10.1016/S0301-6226(01)00269-X

Guitart, R., Sachana, M., Caloni, F., Croubels, S., Vandenbroucke, V., & Berny, P. (2010). Animal poisoning in Europe. Part 3: Wildlife. *Veterinary Journal*, *183*, 260–265. doi:10.1016/j.tvjl.2009.03.033

Gupta, S., & Sinha, A. (2014). A wild boar hunting : predation on a bonnet macaque by a wild boar in the Bandipur National Park , southern India. *Current Science*, *106*, 1186–1187.

Gutterman, Y. (2003). The influences of animal diggings and runoff water on the vegetation in the Negev Desert of Israel. *Israel Journal of Plant Sciences*, *51*, 161–171. doi:10.1560/FLWF-9369-QX08-EY7W

Haaverstad, O., Hjeljord, O., & Wam, H. K. (2014). Wild boar rooting in a northern coniferous forest – minor silviculture impact. *Scandinavian Journal of Forest Research*, *29*, 90–95. doi:10.1080/02827581.2013.865781

Haney, M. J., & Conover, M. R. (2013). Ungulate damage to safflower in Utah. *The Journal of Wildlife Management*, *77*, 282–289. doi:10.1002/jwmg.448

Hanson, L. B., Mitchell, M. S., Grand, J. B., Jolley, D. B., Sparklin, B. D., & Ditchkoff, S. S. (2009). Effect of experimental manipulation on survival and recruitment of feral pigs. *Wildlife Research*, *36*, 185–191. doi:10.1071/WR08077

Harris, J. M., & Cerling, T. E. (2002). Dietary adaptations of extant and Neogene African suids. *Journal of Zoology*, *256*, 45–54. doi:10.1017/S0952836902000067

Hartley, M. (2010). Qualitative risk assessment of the role of the feral wild boar (*Sus scrofa*) in the likelihood of incursion and the impacts on effective disease control of selected exotic diseases in England. *European Journal of Wildlife Research*, *56*, 401–410. doi:10.1007/s10344-009-0334-8

Heard, H., & Stephenson, A. (1987). Electrification of a fence to control the movements of black-backed jackals. *Suid Afrika Tydskrif van Natuurnavorsing*, *17*, 20–24.

Herrero, J., García-Serrano, A., Couto, S., Ortuño, V. M., & García-González, R. (2006). Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. *European Journal of Wildlife Research*, *52*, 245–250. doi:10.1007/s10344-006-0045-3

Higginbottom, K., & King, N. (2006). *The live trade in free- ranging wildlife within South Africa, and implications for Australia*. Rural Industries Research and Development Corporation. Retrieved from https://rirdc.infoservices.com.au/downloads/06-046.

Higgs, J. D. (2000). The changing nature of red meat: 20 years of improving nutritional quality. *Trends in Food Science and Technology*, *11*, 85–95. doi:10.1016/S0924-2244(00)00055-8

Hill, C. M. (2004). Farmers' perspectives of conflict at the wildlife–agriculture boundary: Some lessons learned from african subsistence farmers. *Human Dimensions of Wildlife*, *9*, 279–286. doi:10.1080/10871200490505710

Hoffman, L. C. (2000). The yield and carcass chemical composition of impala (*Aepyceros melampus*), a southern African antelope species, *756*, 752–756.

Hoffman, L. C. (2008). The yield and nutritional value of meat from African ungulates , camelidae , rodents , ratites and reptiles. *Meat Science*, *80*, 94–100. doi:10.1016/j.meatsci.2008.05.018

Hoffman, L. C. (2015). Producing game meat to meet international hygiene and food safety requirements in the bush. In *Annual Reciprocal Meat Conference* (pp. 1–12). Auburn, Alabama, USA.

Hoffman, L. C., & Cawthorn, D.-M. (2012). What is the role and contribution of meat from wildlife in providing high quality protein for consumption? *Animal Frontiers*, *2*, 40–53. doi:10.2527/af.2012-0061

Hoffman, L. C., & Laubscher, L. L. (2010). A comparison between the effects of day and night cropping on gemsbok (*Oryx gazella*) meat quality. *Meat Science*, *85*, 356–362. doi:10.1016/j.meatsci.2010.02.003

Hoffman, L. C., & Sales, J. (2007). Physical and chemical quality characteristics of warthog meat. *Livestock Research for Rural Development*, *19,* 153. Retrieved from http://www.lrrd.org/lrrd19/10/hoff19153.htm

Hoffman, L. C., & Van Schalkwyk, S. (2011). Quality characteristics of blue wildebeest (*Connochaetes taurinus*) meat, *South African Journal of Wildlife Research*, *41*, 210–213.

Hoffman, L. C., & Wiklund, E. (2006). Game and venison – meat for the modern consumer. *Meat Science*, *74*, 197–208. doi:10.1016/j.meatsci.2006.04.005

Hoffman, L. C., Crafford, K., Muller, N., & Schutte, D. W. (2003). Perceptions and consumption of game South Africa. *South African Journal of Wildlife Research*, *33*, 125–130.

Hoffman, L. C., Kroucamp, M., & Manley, M. (2007a). Meat quality characteristics of springbok (*Antidorcas marsupialis*). 1: Physical meat attributes as influenced by age, gender and production region. *Meat Science*, *76*, 755–761. doi:10.1016/j.meatsci.2007.02.017

Hoffman, L. C., Kroucamp, M., & Manley, M. (2007b). Meat quality characteristics of springbok (*Antidorcas marsupialis*). 2: Chemical composition of springbok meat as influenced by age, gender and production region. *Meat Science*, *76*, 762–7. doi:10.1016/j.meatsci.2007.02.018

Hoffman, L. C., Kroucamp, M., & Manley, M. (2007c). Meat quality characteristics of springbok (*Antidorcas marsupialis*). 3: Fatty acid composition as influenced by age, gender and production region. *Meat Science*, *76*, 768–773. doi:10.1016/j.meatsci.2007.02.019

Hoffman, L. C., Kroucamp, M., & Manley, M. (2007d). Meat quality characteristics of springbok (*Antidorcas marsupialis*). 4: Sensory meat evaluation as influenced by age, gender and production region. *Meat Science*, *76*, 774–8. doi:10.1016/j.meatsci.2007.02.020

Hoffman, L. C., Mostert, A C., Kidd, M., & Laubscher, L. L. (2009a). Meat quality of kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*): Carcass yield, physical quality and chemical composition of kudu and impala *Longissimus dorsi* muscle as affected by gender and age. *Meat Science*, *83*, 788–95. doi:10.1016/j.meatsci.2009.08.022

Hoffman, L. C., Mostert, A. C., & Laubscher, L. L. (2009c). Meat quality of kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*): The effect of gender and age on the fatty acid profile, cholesterol content and sensory characteristics of kudu and impala meat. *Meat Science*, *83*, 737–743. doi:10.1016/j.meatsci.2009.08.026

Hoffman, L. C., Muller, M., Schutte, D. W., & Crafford, K. (2004). The retail of South African game meat : current trade and marketing trends. *South African Journal of Wildlife Research*, *34*, 123–134.

Hoffman, L. C., Muller, M., Schutte, D. W., Calitz, F. J., & Crafford, K. (2005). Consumer expectations , perceptions and purchasing of South African game meat. *South African Journal of Wildlife Research*, *35*, 33–42.

Hoffman, L. C., Smit, K., & Muller, N. (2008). Chemical characteristics of blesbok (*Damaliscus dorcas phillipsi*) meat. *Journal of Food Composition and Analysis*, *21*, 315–319. doi:10.1016/j.jfca.2007.12.003

Hoffman, L. C., Van Schalkwyk, S. & Müller, N. (2009b). Effect of season and gender on the physical and chemical composition of black wildebeest (*Connochaetus gnou*) meat, *39*, 170–174.

Hoffman, L. C., Vosloo, C., Nkhabutlane, P., & Schutte, D. W. (2005). Associations with rabbits and rabbit meat of three different ethnic groups in Stellenbosch , South Africa. *Journal of Family Ecology and Consumer Sciences*, *33*, 63–72.

Hoffman, L., Smit, K., & Muller, N. (2010). Chemical characteristics of red hartebeest (*Alcelaphus buselaphus caama*) meat. *South African Journal of Animal Science*, *40*, 221–228. Retrieved from http://www.scielo.org.za/scielo.php?pid=S0375-15892010000300008&script=sci_arttext

Holmgren, M. (2002). Exotic herbivores as drivers of plant invasion and switch to ecosystem alternative states. *Biological Invasions, 45*, 25–33.

Hone, J. (2002). Feral pigs in Namadgi National Park, Australia: Dynamics, impacts and management. *Biological Conservation*, *105*, 231–242. doi:10.1016/S0006-3207(01)00185-9

Hone, J., & Atkinson, B. (1983). Evaluation of fencing to control feral pig movement. *Australia Wildlife Research*, *10*, 499–505.

Hone, J., & Stone, C. P. (1989). A comparison and evaluation of feral pig management in two national parks. *Wildlife Society Bulletin*, *17*, 419–425. doi:10.2307/3782705

Honikel, K. O. (2004). Conversion of muscle to meat: Glycolysis. In W. K. Jensen, D. Carrick, & M. Dikeman. (Eds.) *Encyclopedia of Meat Sciences* (pp. 314–318). Oxford, UK: Elsevier Ltd.

Huff-Lonergan, E., & Lonergan, S. M. (2005). Mechanisms of water-holding capacity of meat: The role of postmortem biochemical and structural changes. *Meat Science*, *71*, 194–204. doi:10.1016/j.meatsci.2005.04.022

Hummel, J., Findeisen, E., Sudekum, K.-H., Ruf, I., Kaiser, T. M., Bucher, M., … Codron, D. (2011). Another one bites the dust: faecal silica levels in large herbivores correlate with high-crowned teeth. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 1742–1747. doi:10.1098/rspb.2010.1939

Hunter, L. T. B. (1998). *The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, KwaZulu Natal, South Africa*. MSc thesis, University of Pretoria, Pretoria, South Africa.

Hyytiäinen, H. K., Mykkänen, A. K., Hielm-Björkman, A. K., Stubbs, N. C., & McGowan, C. M. (2014). Muscle fibre type distribution of the thoracolumbar and hindlimb regions of horses: relating fibre type and functional role. *Acta Veterinaria Scandinavica*, *56*, 8. doi:10.1186/1751-0147-56-8

Immonen, K., Ruusunen, M., Hissa, K., & Puolanne, E. (2000). Bovine muscle glycogen concentration in relation to finishing diet, slaughter and ultimate pH. *Meat Science*, *55*, 25–31. doi:S0309-1740(99)00121-7 [pii]

Issanchou, S. (1996). Consumer expectations and perceptions of meat and meat product quality. *Meat Science*, *43*, 5–19. doi:10.1016/0309-1740(96)00051-4

IUCN/SSC. (2013). *Guidelines for Reintroductions and Other Conservation Translocations. IUCN Guidelines for Reintroductions and Other Conservation Translocations*.Version 1.0. Gland, Switzerland: IUCN Species Survival Commission.

Jenkins, T. C. (1993). Lipid metabolism in the rumen. *Journal of Dairy Science*, *76*, 3851–3863. doi:10.1016/0079-6832(78)90004-6

Jeremiah, L. E., Dugan, M. E. R., Aalhus, J. L., & Gibson, L. L. (2003). Assessment of the chemical and cooking properties of the major beef muscles and muscle groups. *Meat Science*, *65*, 985–992. doi:10.1016/S0309-1740(02)00308-X

Jeschke, J. M. (2008). Across islands and continents, mammals are more successful invaders than birds. *Diversity and Distributions*, *14*, 913–916. doi:10.1111/j.1472-4642.2008.00488.x

Jeschke, J. M., & Strayer, D. L. (2005). Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 7198–202. doi:10.1073/pnas.0501271102

Jezierski, W. (1977). Longevity and mortality rate in a population of wild boar. *Acta Theriologica*, *22*, 337–348.

Jori, F., Brahmbhatt, D., Fosgate, G. T., Thompson, P. N., Budke, C., Ward, M. P., … Gummow, B. (2011). A questionnaire-based evaluation of the veterinary cordon fence separating wildlife and livestock along the boundary of the Kruger National Park, South Africa. *Preventive Veterinary Medicine*, *100*, 210–220. doi:10.1016/j.prevetmed.2011.03.015

Kadim, I. T., Mahgoub, O., Al-Ajmi, D. S., Al-Maqbaly, R. S., Al-Mugheiry, S. M., & Bartolome, D. Y. (2004). The influence of season on quality characteristics of hot-boned beef m. *Longissimus thoracis*. *Meat Science*, *66*, 831–836. doi:10.1016/j.meatsci.2003.08.001

Kadim, I. T., Mahgoub, O., Al-Marzooqi, W., Al-Ajmi, D. S., Al-Maqbali, R. S., & Al-Lawati, S. M. (2008). The influence of seasonal temperatures on meat quality characteristics of hot-boned, m. *psoas* major and minor, from goats and sheep. *Meat Science*, *80*, 210–215. doi:10.1016/j.meatsci.2007.11.022

Kagoro-Rugunda, G. (2004). Crop raiding around Lake Mburo National Park, Uganda. *African Journal of Ecology*, *42*, 32–41. doi:10.1111/j.0141-6707.2004.00444.x

Kane, D. E., & Hellberg, R. S. (2016). Identification of species in ground meat products sold on the U.S. commercial market using DNA-based methods. *Food Control*, *59*, 158–163. doi:10.1016/j.foodcont.2015.05.020

Kang, Y. K., Choi, Y. M., Lee, S. H., Choe, J. H., Hong, K. C., & Kim, B. C. (2011). Effects of myosin heavy chain isoforms on meat quality, fatty acid composition, and sensory evaluation in Berkshire pigs. *Meat Science*, *89*, 384–389. doi:10.1016/j.meatsci.2011.04.019

Karanth, K. K., Naughton-Treves, L., Defries, R., & Gopalaswamy, A. M. (2013). Living with wildlife and mitigating conflicts around three Indian protected areas. *Environmental Management*, *52*, 1320–32. doi:10.1007/s00267-013-0162-1

Karlsson, A., & Klont, R. (1999). Skeletal muscle fibres as factors for pork quality. *Livestock Production Science*, *42*, 415–431. doi:10.1051/rnd

Kassilly, F. N., Tsingalia, H. M., & Gossow, H. (2008). Mitigating human-wildlife conflicts through wildlife fencing: A Kenyan case study. *Wildlife Biology in Practice*, *4*, 30–38. doi:10.2461/wbp.2008.4.3

Kaswamila, A., Russell, S., & McGibbon, M. (2007). Impacts of wildlife on household food security and income in Northeastern Tanzania. *Human Dimensions of Wildlife*, *12*, 391–404. doi:10.1080/10871200701670003

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, *17*, 164–170.

Kearney, J. (2010). Food consumption trends and drivers. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*, 2793–807. doi:10.1098/rstb.2010.0149

Keeton, J.T. & Eddy, S. (2004). Chemical and physical characteristics of meat/Chemical composition. In W. K. Jensen, D. Carrick, & M. Dikeman, M. (Eds.) *Encyclopedia of meat sciences* (pp. 210–218). Oxford, UK: Elsevier Ltd.

Kelly, D. W., Paterson, R. A., Townsend, C. R., Poulin, R., & Tompkins, D. M. (2015). Parasite spillback: A neglected concept in invasion ecology. *Ecology*, *90*, 2047–2056. doi:10.2307/41739371

Kesch, K. M., Bauer, D. T., & Loveridge, A. J. (2013). Undermining game fences : who is digging holes in Kalahari sands ? *African Journal of Ecology*, *52*, 144–150.

Keuling, O., Baubet, E., Duscher, A., Ebert, C., Fischer, C., Monaco, A., … Thurfjell, H. (2013). Mortality rates of wild boar *Sus scrofa* L. in central Europe. *European Journal of Wildlife Research*, *59*, 805–814. doi:10.1007/s10344-013-0733-8

Kiberd, P. (2006). Bundu farm: A report on archaeological and palaeoenvironemental assemblages from a pan site in Bushmanland, Northern Cape, South Africa. *South African Archaeological Bulletin*, *61*, 189–201.

Kiley-Worthington, M. (2014). Ecological agriculture . Integrating low input, high productive farming with wildlife conservation. Results from the experimental farm La Combe , Drome France. *Open Journal of Ecology*, *4*, 744–763.

Kingdon, J. (1997). *The Kingdon field guide to African mammals*. (1st ed.). London, England: Academic Press Limited.

Kjällstrand, J., & Petersson, G. (2001). Phenolic antioxidants in wood smoke. *Science of The Total Environment*, *277*, 69–75. doi:10.1016/S0048-9697(00)00863-9

Klein, R. G. (1988). The archaeological bones from Acheulean significance sites of animal in southern Africa. *The African Archaeological Review*, *6*, 3–25.

Kleynhans, E. J., Jolles, A. E., Bos, M. R. E., & Olff, H. (2011). Resource partitioning along multiple niche dimensions in differently sized African savanna grazers. *Oikos*, *120*, 591–600. doi:10.1111/j.1600-0706.2010.18712.x

Koichi, K., Cottrell, A., Sangha, K. K., & Gordon, I. J. (2013). What determines the acceptability of wildlife control methods? A case of feral pig management in the Wet Tropics World Heritage Area, Australia. *Human Dimensions of Wildlife*, *18*, 97–108. doi:10.1080/10871209.2013.727523

Kolar, C. S., & Lodge, D. M. (2001). Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution*, *16*, 199–204. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11245943

Kondaiah, N. (2004). Value added meat products and development of processed meat sector. *Natural Product Radiance*, *3*, 281–283.

Koster, J. M., Hodgen, J. J., Venegas, M. D., & Copeland, T. J. (2010). Is meat flavor a factor in hunters' prey choice decisions? *Human Nature*, *21*, 219–242. doi:10.1007/s12110-010-9093-1

Koval, M. H., & Mertig, A. G. (2004). Attitudes of the Michigan public and wildlife agency personnel toward lethal wildlife management. *Wildlife Society Bulletin*, *32*, 232–243. doi:10.2193/0091-7648(2004)32[232:AOTMPA]2.0.CO;2

Kraft, A. A. (1992). Psychotropic bacteria in foods: Disease and spoilage. Boca Raton, USA: CRC Press.

Kristensen, L., Støier, S., Würtz, J., & Hinrichsen, L. (2014). Trends in meat science and technology: the future looks bright, but the journey will be long. *Meat Science*, *98*, 322–9. doi:10.1016/j.meatsci.2014.06.023

Kritzinger, B., Hoffman, L. C., & Ferreira, A. V. (2004). A comparison between the effects of two cropping methods on the meat quality of impala (*Aepyceros melampus*). *South African Journal of Animal*, *33*, 233–241. Retrieved from http://www.ajol.info/index.php/sajas/article/view/3779

Kroon, F. E., Van Rensburg, W. J. J., & Hofmeyr, H. S. (1972). Seisoenale veranderinge in chemiese samestelling van volwasse blesbokramme (*Damaliscus dorcas phillipsi*) van die van Riebeeck Natuurreservaat. *Suid-Afrikaanse Tydskrif Vir Veekunde*, *2*, 41–44.

Kušec, Kralik, Đurkin, Petričević, & Hanžek, D. (2007). Factors discriminating between pork quality conditions. *Poljoprivreda / Agriculture*, *13*, 66–69.

Lavelle, M. J., Vercauteren, K. C., Hefley, T. J., Phillips, G. E., Hygnstrom, S. E., Long, D. B., … Campbell, T. A. (2011). Evaluation of fences for containing feral swine under simulated depopulation conditions. *The Journal of Wildlife Management*, *75*, 1200–1208. doi:10.1002/jwmg.134

Lawrie, R. A., & Ledward, D. A. (2006). *Lawrie's meat science* (7th ed.). Cambridge, England: Woodhead Publishing.

Lindsey, P. A., Havemann, C. P., Lines, R. M., Price, A. E., Retief, T. A., Rhebergen, T., … Romañach, S. S. (2013). Benefits of wildlife-based land uses on private lands in Namibia and limitations affecting their development. *Oryx*, *47*, 41–53. doi:10.1017/S0030605311001049

Lindsey, P. A., Masterson, C. L., Beck, A. L., & Romañach, S. S. (2012). Fencing for conservation. In M. J. Somers & M. W. Haywards (Eds.), *Fencing for Conservation: Restriction of Evolutionary Potential or a Riposte to Threatening Processes?* (pp. 215–234). Springer Science and Business Media. doi:10.1007/978-1-4614-0902-1

Linkie, M., Dinata, Y., Nofrianto, A., & Leader-Williams, N. (2007). Patterns and perceptions of wildlife crop raiding in and around Kerinci Seblat National Park, Sumatra. *Animal Conservation*, *10*, 127–135. doi:10.1111/j.1469-1795.2006.00083.x

Ljung, P. E., Riley, S. J., Heberlein, T. a., & Ericsson, G. (2012). Eat prey and love: Game-meat consumption and attitudes toward hunting. *Wildlife Society Bulletin*, *36*, 669–675. doi:10.1002/wsb.208

Lomiwes, D., Farouk, M. M., Wu, G., & Young, O. A. (2014). The development of meat tenderness is likely to be compartmentalised by ultimate pH. *Meat Science*, *96*, 646–51. doi:10.1016/j.meatsci.2013.08.022

Long, K., & Robley, A. (2004). *Cost effective feral animal exclusion fencing for areas of high conservation value in Australia*. Melbourne, Australia: Department of the Environmental And Heritage, Australian Government.

Lönnberg, E. (1908). Remarks on some wart-hog skulls in the British Museum. *Proceedings of the Zoological Society of London*, *78*, 936–940.

Lowe, S., Browne, M., Boudjelas, S., & De Poorter, M. (2000). *100 of the world's worst invasive alien species: A selection from the global invasive species database*. The Invasive Species Survival Commission (SSC) of the World Conservation Union (IUCN).

Lowney, M., Schoenfeld, P., Haglan, W., & Witmer, G. (2005). Overview of impacts of feral and introduced ungulates on the environment in the eastern United States and Caribbean. In D. L. Nolte & K. A. Fagerstone (Eds.), *Wildlife Damage Management Conferences – Proceedings*, paper 88. Retrieved from http://digitalcommons.unl.edu/icwdm_wdmconfproc/88/

Luskin, M. S., Christina, E. D., Kelley, L. C., & Potts, M. D. (2014). Modern hunting practices and wild meat trade in the oil palm plantation-dominated landscapes of Sumatra, Indonesia. *Human Ecology*, *42*, 35–45. doi:10.1007/s10745-013-9606-8

Macci, C., Doni, S., Bondi, G., Davini, D., Masciandaro, G., & Pistoia, A. (2012). Effects of wild boar (*Sus scrofa*) grazing on soil properties in Mediterranean environment. *Catena*, *98*, 79–86. doi:10.1016/j.catena.2012.06.005

Maciejewski, K., & Kerley, G. I. H. (2014). Understanding tourists' preference for mammal species in private protected areas: is there a case for extralimital species for ecotourism? *PloS One*, *9*, e88192. doi:10.1371/journal.pone.0088192

MacMillan, D. C., & Phillip, S. (2008). Consumptive and non-consumptive values of wild mammals in Britain. *Mammal Review*, *38*, 189–204. doi:10.1111/j.1365-2907.2008.00124.x

Madden, F. (2004). Creating coexistence between humans and wildlife: Global perspectives on local efforts to address human–wildlife conflict. *Human Dimensions of Wildlife*, *9*, 247–257. doi:10.1080/10871200490505675

Magwedere, K., Sithole, F., Hoffman, L. C., Hemberger, Y. M., & Dziva, F. (2013). Investigating the contributing factors to postmortem pH changes in springbok, eland, red hartebeest and kudu edible offal. *Journal of the South African Veterinary Association*, *84*, E1–7. doi:10.4102/jsava.v84i1.919

Maltin, C., Balcerzak, D., Tilley, R., & Delday, M. (2003). Determinants of meat quality: tenderness. *Proceedings of the Nutrition Society*, *62*, 337–347. doi:10.1079/PNS2003248

Mamo, D., Bouer, H., & Tesfay, Y. (2013). Crop damage by African elephants assessment in Kaftasheraro National park, Ethiopia. *African Journal of Ecology*, 138–143. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/aje.12094/full

Mancini, R. A., & Hunt, M. C. (2005). Current research in meat color. *Meat Science*, *71*, 100–121. doi:10.1016/j.meatsci.2005.03.003

Marchiori, A., & Felício, P. (2003). Quality of wild boar meat and commercial pork. *Scientia Agricola*, *60*, 1–5. Retrieved from http://www.scielo.br/scielo.php?pid=S0103-90162003000100001&script=sci_arttext

Marino, R., Albenzio, M., della Malva, A., Muscio, A., & Sevi, A. (2015). Nutritional properties and consumer evaluation of donkey bresaola and salami: Comparison with conventional products. *Meat Science*, *101*, 19–24. doi:10.1016/j.meatsci.2014.11.001

Marquez, M. J., & Boecklen, W. J. (2010). Isotopic shift in an introduced population of gemsbok (*Oryx gazella*). *Journal of Arid Environments*, *74*, 928–932. doi:10.1016/j.jaridenv.2010.01.004

Mason, D. R. (1982). *Studies on the biology and ecology of the warthog Phacochoerus aethiopicus sundevalli Lönnberg, 1908 in Zululand, South Africa*. DSc Thesis, University of Pretoria, Pretoria, South Africa.

Massei, G., Genov, P. V., Staines, B. W., & Gorman, M. L. (1997). Mortality of wild boar, *Sus scrofa*, in a Mediterranean area in relation to sex and age. *Journal of Zoology*, *242*, 394–400.

Massei, G., Sugoto, R., & Bunting, R. (2011). Too many hogs ? A review of methods to mitigate impact by wild boar and feral hogs. *Human-Wildlife Interactions*, *5*, 79–99.

Matthee, S., Swanepoel, M., Van der Mescht, L. Van Der, Leslie, A. J., & Hoffman, L. C. (2013). Ectoparasites of a non-indigenous warthog population, *Phacochoerus africanus*, in the Free State Province, South Africa. *South African Journal of Wildlife Research*, *48*, 259–265. doi:10.3377/004.048.0210

Mayer, J. J. (2013). Wild pig attacks on humans. In J. B. Armstrong & G. R. Gallagher (Eds.), *Wildlife Damage Management Conferences – Proceedings,* 17–35. Retrieved from http://digitalcommons.unl.edu/icwdm_wdmconfproc/151.

McCann, B. E., & Garcelon, D. K. (2008). Eradication of feral pigs from Pinnacles National Monument. *Journal of Wildlife Management*, *72*, 1287–1295. doi:10.2193/2007-164

McIvor, D., & Conover, M. (1994). Perceptions of farmers and non-farmers toward management of problem wildlife. *Wildlife Society Bulletin*, *22*, 212–219.

McKinney, M. L. (2005). Species introduced from nearby sources have a more homogenizing effect than species from distant sources: evidence from plants and fishes in the USA. *Diversity and Distributions*, *11*, 367–374. doi:10.1111/j.1366-9516.2005.00181.x

McManus, J. S., Dickman, A. J., Gaynor, D., Smuts, B. H., & Macdonald, D. W. (2014). Dead or alive? Comparing costs and benefits of lethal and non-lethal human–wildlife conflict mitigation on livestock farms. *Oryx*, 1–9. doi:10.1017/S0030605313001610

Mendoza, M., & Palmqvist, P. (2008). Hypsodonty in ungulates: an adaptation for grass consumption or for foraging in open habitat? *Journal of Zoology*, *274*, 134–142. doi:10.1111/j.1469-7998.2007.00365.x

Meng, X. J., Lindsay, D. S., & Sriranganathan, N. (2009). Wild boars as sources for infectious diseases in livestock and humans. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 364*, 2697–707. doi:10.1098/rstb.2009.0086.

Mfunda, I. M., & Røskaft, E. (2011). Wildlife or crop production: the dilemma of conservation and human livelihoods in Serengeti, Tanzania. *International Journal of Biodiversity Science, Ecosystem Services & Management*, *7*, 39–49. doi:10.1080/21513732.2011.602028

Mgqatsa, N. (2010). *Diet and population trends of warthog in the Addo Elephant National Park*. MSc thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

Mkanda, F. X., & Chansa, W. (2011). Changes in temporal and spatial pattern of road kills along the Lusaka-Mongu (M9) highway , Kafue National Park , Zambia. *South African Journal of Wildlife Research*, *41*, 68–76.

Mokotjomela, T. M., Musil, C. F., & Esler, K. J. (2013). Do frugivorous birds concentrate their foraging activities on those alien plants with the most abundant and nutritious fruits in the South African Mediterranean-climate region? *Plant Ecology*, *214*, 49–59. doi:10.1007/s11258-012-0145-y

Monin, G. (2004). Conversion of muscle to meat: Colour and texture deviations. In W. K. Jensen, D. Carrick, & M. Dikeman, M. (Eds.) *Encyclopedia of Meat Sciences* (pp. 323–330). Oxford, UK: Elsevier Ltd.

Moreno-Opo, R., Ould Sidaty, Z. E., Baldò, J. M., Garcìa, F., Ould Sehla Daf, D., & Gonzàlez, L. M. (2013). A breeding colony of the Near Threatened Lesser Flamingo Phoeniconaias minor in western Africa: a conservation story of threats and land management. *Bird Conservation International*, *23*, 426–436. doi:10.1017/S0959270912000366

Morton, F., & Hitchcock, R. (2014). Tswana hunting: Continuities and changes in the Transvaal and Kalahari after 1600. *South African Historical Journal*, *66*, 418–439. doi:10.1080/02582473.2013.855809

Mostert, R., & Hoffman, L. C. (2007). Effect of gender on the meat quality characteristics and chemical composition of kudu (*Tragelaphus strepsiceros*), an African antelope species. *Food Chemistry*, *104*, 565–570. doi:10.1016/j.foodchem.2006.12.006

Mottram, D. S. (1998). Flavour formation in meat and meat products : A review. *Food Chemistry*, *62*, 415-424.

Mukaratirwa, S., La Grange, L., & Pfukenyi, D. M. (2013). Trichinella infections in animals and humans in sub-Saharan Africa: A review. *Acta Tropica*, *12*, 82–89. doi:10.1016/j.actatropica.2012.09.005

Muwanika, V. B., Nyakaana, S., & Siegismund, H. R. (2006). Population genetic structure of the common warthog (*Phacochoerus africanus*) in Uganda : evidence for a strong philopatry among warthogs and social structure breakdown in a disturbed population. *African Journal of Ecology*, *45*, 22–30.

Muwanika, V. B., Nyakaana, S., Siegismund, H. R., & Arctander, P. (2003). Phylogeography and population structure of the common warthog (*Phacochoerus africanus*) inferred from variation in mitochondrial DNA sequences and microsatellite loci. *Heredity*, *91*, 361–72. doi:10.1038/sj.hdy.6800341

Mworia, J. K., Kinyamario, J. I., Omari, J. K., & Wambua, J. K. (2011). Patterns of seed dispersal and establishment of the invader Prosopis juliflora in the upper floodplain of Tana River, Kenya. *African Journal of Range & Forage Science*, *28*, 35–41. doi:10.2989/10220119.2011.571402

Mysterud, A. (2010). Still walking on the wild side? Management actions as steps towards "semi-domestication" of hunted ungulates. *Journal of Applied Ecology*, *47*, 920–925. doi:10.1111/j.1365-2664.2010.01836.x

Naughton-Treves, L. (1998). Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conservation Biology*, *12*, 156–168. doi:10.1046/j.1523-1739.1998.96346.x

Neethling, J., Britz, T. J., & Hoffman, L. C. (2014). Impact of season on the fatty acid profiles of male and female blesbok (*Damaliscus pygargus phillipsi*) muscles. *Meat Science*, *98*, 599–606. doi:10.1016/j.meatsci.2014.06.030

Neethling, J., Hoffman, L. C., & Britz, T. J. (2013). Impact of season on the chemical composition of male and female blesbok (*Damaliscus pygargus phillipsi*) muscles. *Journal of the Science of Food and Agriculture*, *94*, 424–431. doi:10.1002/jsfa.6281

Neubert, M. G., & Caswell, H. (2000). Demography and dispersal: Calculation and sensivity analysis of invasion speed for structured populations. *Ecology*, *6*, 1613–1628.

Nogueira, S. S. D. C., Nogueira-Filho, S. L. G., Bassford, M., Silvius, K., & Fragoso, J. M. V. (2007). Feral pigs in Hawai'i: Using behavior and ecology to refine control techniques. *Applied Animal Behaviour Science*, *108*, 1–11. doi:10.1016/j.applanim.2007.03.011

North, M. K., & Hoffman, L. C. (2015). Changes in springbok (*Antidorcas marsupialis) Longissimus thoracis et lumborum* muscle during conditioning as assessed by a trained sensory panel. *Meat Science*, *108*, 1–8. doi:10.1016/j.meatsci.2015.05.004

North, M. K., Frylinck, L., & Hoffman, L. C. (2015). The physical and biochemical changes in springbok (*Antidorcas marsupialis*) *Longissimus thoracis et lumborum* and *Biceps femoris* muscle during ageing. *Meat Science*, *110*, 145–152. doi:10.1016/j.meatsci.2015.07.009

North, M. K., Frylinck, L., & Hoffman, L. C. (2016). The changes in springbok (*Antidorcas marsupialis*) *Longissimus thoracis et lumborum* and *Biceps femoris* muscle during the rigour period. *Meat Science*, *110*, 145–152. doi:10.1016/j.meatsci.2015.07.009

Nuñez, M. A., Kuebbing, S., Dimarco, R. D., & Simberloff, D. (2012). Invasive Species: to eat or not to eat, that is the question. *Conservation Letters*, *5*, 334–341. doi:10.1111/j.1755-263X.2012.00250.x

Nyafu, K. (2009). *Warthog as an introduced species in the Eastern Cape*. MSc thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

Nyakaana, S., Abe, E., Arctander, P., & Siegismund, H. (2001). DNA evidence for elephant social behaviour breakdown in Queen Elizabeth National Park, Uganda. *Animal Conservation*, *4*, 231–237. doi:10.1017/S1367943001001275

Nyirenda, V. R., Chansa, W. C., Myburgh, W. J., & Reilly, B. K. (2011). Wildlife crop depredation in the Luangwa Valley, eastern Zambia. *Journal of Ecology and the Natural Environment*, *3*, 481–491. doi:10.5897/JENE11.094

O'Connor, T. G., & Kuyler, P. (2009). Impact of land use on the biodiversity integrity of the moist sub-biome of the grassland biome, South Africa. *Journal of Environmental Management*, *90*, 384–395. doi:10.1016/j.jenvman.2007.10.012

Obanda, V. O., Lekolool, I., Munyao, M., Chege, S. M., Manyibe, T., & Gakuya, F. (2011). New distribution records for the desert Warthog (*Phacochoerus aethiopicus delamerei* - Pallas 1766). *African Journal of Ecology*, *49*, 373–376.

Odadi, W. O., Karachi, M. K., Abdulrazak, S. a, & Young, T. P. (2011). African wild ungulates compete with or facilitate cattle depending on season. *Science, 333*, 1753–1755. doi:10.1126/science.1208468

Ogada, D. L. (2014). The power of poison: Pesticide poisoning of Africa's wildlife. *Annals of the New York Academy of Sciences*, *1322*, 1–20. doi:10.1111/nyas.12405

Oja, R., Kaasik, A., & Valdmann, H. (2014). Winter severity or supplementary feeding—which matters more for wild boar? *Acta Theriologica*, *59*, 553–559. doi:10.1007/s13364-014-0190-0

Onyango, C. A., Izumimoto, M., & Kutima, P. M. (1998). Comparison some physical and comparison of some physical and chemical properties of selected game meats. *Meat Science*, *49*, 117–125.

Otali, E., & Gilchrist, J. S. (2004). The effcts of refuse feeding on body condition, reproduction, and survial of naded mongooses. *Journal of Mammalogy*, *85*, 491–497.

Owen-Smith, N., & Chafota, J. (2012). Selective feeding by a megaherbivore, the African elephant (*Loxodonta africana*). *Journal of Mammalogy*, *93*, 698–705. doi:10.1644/11-MAMM-A-350.1

Paleari, M. A., Moretti, V. M., Beretta, G., Mentasti, T., & Bersani, C. (2003). Cured products from different animal species. *Meat Science*, *63*, 485–9. doi:10.1016/S0309-1740(02)00108-0

Parkes, J. P., Ramsey, D. S. L., Macdonald, N., Walker, K., McKnight, S., Cohen, B. S., & Morrison, S. A. (2010). Rapid eradication of feral pigs (*Sus scrofa*) from Santa Cruz Island, California. *Biological Conservation*, *143*, 634–641. doi:10.1016/j.biocon.2009.11.028

Parkes, J., & Murphy, E. (2003). Management of introduced mammals in New Zealand. *New Zealand Journal of Zoology*, *30*, 335–359. Retrieved from http://www.tandfonline.com/doi/abs/10.1080/03014223.2003.9518346

Pavlov, P. M., & Hone, J. (1982). The Behaviour of feral pigs, *Sus scrofa*, in flocks of lambing ewes. *Australia Wildlife Research*, *9*, 101–109.

Penzhorn, B. L. (1971). A summary of the reintroduction of ungulates into South African National Parks (to 31 December 1970). *Koedoe*, *14*, 145–159.

Perez, J. (2005). Hogs gone wild! *Journal of Agricultural & Food Information*, *6*, 161–166. doi:10.1300/J108v06n02_12

Pietersen, D. W., Mckechnie, A. E., & Jansen, R. (2014). A review of the anthropogenic threats faced by Temminck ' s ground pangolin, *Smutsia temminckii*, in southern Africa. *South African Journal of Wildlife Research*, *44*, 167–178.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., … Tsomondo, T. (2001). Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environment*, *84*, 1–20. doi:10.1016/S0167-8809(00)00178-X

Pittiglio, C., Skidmore, A. K., van Gils, H. A M. J., McCall, M. K., & Prins, H. H. T. (2014). Smallholder farms as stepping stone corridors for crop-raiding elephant in northern Tanzania: integration of Bayesian expert system and network simulator. *Ambio*, *43*, 149–61. doi:10.1007/s13280-013-0437-z

Plesner-Jensen, S., Siefert, L., Okori, J. J. L., & Clutton-Brock, T. H. (1999). Age-related participation in allosuckling by nursing warthogs (*Phacochoerus africanus*). *Journal of Zoology*, *248*, 443–449. doi:10.1017/S0952836999008043

Poligne, I., Collignan, A., & Trystram, G. (2002). Effects of salting, drying, cooking, and smoking operations on volatile compound formation and color patterns in pork. *Journal of Food Science*, *67*, 2976–2986. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2621.2002.tb08848.x/abstract

Pollard, J. C., Littlejohn, R. P., Asher, G. W., Pearse, A. J. T., Stevenson-Barry, J. M., McGregor, S. K., … Prescott, J. (2002). A comparison of biochemical and meat quality variables in red deer (*Cervus elaphus*) following either slaughter at pasture or killing at a deer slaughter plant. *Meat Science*, *60*, 85–94. doi:10.1016/S0309-1740(01)00110-3

Poshiwa, X., Groeneveld, R. A., Heitkönig, I. M. A., & Prins, H. H. T. (2013). Reducing rural households ' annual income fluctuations due to rainfall variation through diversification of wildlife use : portfolio theory in a case study of south eastern Zimbabwe . *Tropical Conservation Science*, *6*, 201–220.

Post, E., & Stenseth, N. C. (1999). Climate variability, plant phenology, and northern ungulates. *Ecology*, *80*, 1322–1339.

Professional Hunters Association of South Africa (PHASA). (2014). *Revenue from hunting tourists breaks R1 billion mark.* Retrieved from www.phasa.co.za/what-is-in-the-news/phasa-press-release/item/570-revenue-from-hunting-tourists-breaks-r1-billion-mark.html.

Purslow, P. P. (2005). Intramuscular connective tissue and its role in meat quality. *Meat Science*, *70*, 435–447. doi:10.1016/j.meatsci.2004.06.028

Quaresma, M. A. G., Alves, S. P., Trigo-Rodrigues, I., Pereira-Silva, R., Santos, N., Lemos, J. P. C., … Bessa, R. J. B. (2011). Nutritional evaluation of the lipid fraction of feral wild boar (*Sus scrofa*) meat. *Meat Science*, *89*, 457–461. doi:10.1016/j.meatsci.2011.05.005

Quinto, C. A., Tinoco, R., & Hellberg, R. S. (2016). DNA barcoding reveals mislabeling of game meat species on the U.S. Commercial Market. *Food Control*, *59*, 386–392. doi:10.1016/j.foodcont.2015.05.043

Quirin, C., & Dixon, A. (2012). Food security, politics and perceptions of wildlife damage in Western Ethiopia. *International Journal of Pest Management*, *58*, 101–114. doi:10.1080/09670874.2012.667583

Radder, L., & le Roux, R. (2005). Factors affecting food choice in relation to venison: A South African example. *Meat Science*, *71*, 583–589. doi:10.1016/j.meatsci.2005.05.003

Radloff, F. G. T., Van der Waal, C., & Bond, A. L. (2013). Extensive browsing by a conventional grazer? Stable carbon isotope analysis reveals extraordinary dietary flexibility among Sanga cattle of North Central Namibia. *Isotopes in Environmental and Health Studies*, *49*, 318–24. doi:10.1080/10256016.2013.789025

Raffaele, E., Veblen, T. T., Blackhall, M., & Tercero-Bucardo, N. (2011). Synergistic influences of introduced herbivores and fire on vegetation change in northern Patagonia, Argentina. *Journal of Vegetation Science*, *22*, 59–71. doi:10.1111/j.1654-1103.2010.01233.x

Randi, E., D'Huart, J.-P., Lucchini, V., & Aman, R. (2002). Evidence of two genetically deeply divergent species of warthog, *Phacochoerus africanus* and *P . aethiopicus* (Artiodactyla : Suiformes) in East Africa. *Mammalian Biology - Zeitschrift Für Säugetierkunde*, *67*, 91–96.

Rautenbach, I. L. (1982). *Mammals of the Transvaal*. Pretoria, South Africa: Ecoplan.

Rehfeldt, C., Stickland, N. C., Fiedler, I., & Wegner, J. (1999). Environmental and genetic factors as sources of variation in skeletal muscle fibre number. *Basic Applied Myology, 9*, 235-253.

Reidy, M. M., Campbell, T. A., & Hewitt, D. G. (2008). Evaluation of electric fencing to inhibit feral pig movements. *Journal of Wildlife Management*, *72*, 1012–1018. doi:10.2193/2007-158

Reiter, D. K., Brunson, M. W., & Schmidt, R. H. (1999). Public attitudes toward wildlife damage management and policy. *Wildlife Society Bulletin*, *27*, 746–758.

Riley, S., Siemer, W., Decker, D., Carpenter, L., Organ, J., & Berchielli, L. (2003). Adaptive impact management: An integrative approach to wildlife management. *Human Dimensions of Wildlife*, *8*, 81–95. doi:10.1080/10871200304301

Rincker, P., & Bechtel, P. (2006). Similarities and differences in composition and selected sensory attributes of reindeer, caribou and beef. *Journal of Muscle Foods*, *17*, 65–78. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.1745-4573.2006.00036.x/full

Risch, A. C., Wirthner, S., Busse, M. D., Page-Dumroese, D. S., & Schütz, M. (2010). Grubbing by wild boars (*Sus scrofa* L.) and its impact on hardwood forest soil carbon dioxide emissions in Switzerland. *Oecologia*, *164*, 773–84. doi:10.1007/s00442-010-1665-6

Roberts, A. (1951). *The mammals of South Africa*. (1st ed.). In R. Bigalke, V. Fitzsimons & D. E. Malan (Eds.), (pp. 267-269). South Africa: Trustees of The mammals of South Africa Book Fund.

Roberts, B. A. (2012). An attack by a warthog *Phacochoerus africanus* on a newborn Thomson's gazelle *Gazella thomsonii*. *African Journal of Ecology*, *50*, 507–508. doi:10.1111/j.1365-2028.2012.01344.x

Rødbotten, M., Kubberød, E., Lea, P., & Ueland, O. (2004). A sensory map of the meat universe: Sensory profile of meat from 15 species. *Meat Science*, *68*, 137–44. doi:10.1016/j.meatsci.2004.02.016

Roman, J. (2005, September). We shall eat them on the beaches ; We've a talent for eating species to extinction, so why not put it to good use for a change. *New Scientist*, 41–44.

Saadoun, A., & Cabrera, M. C. (2008). A review of the nutritional content and technological parameters of indigenous sources of meat in South America. *Meat Science*, *80*, 570–81. doi:10.1016/j.meatsci.2008.03.027

Sales, J., & Kotrba, R. (2013). Meat from wild boar (Sus scrofa L.): A review. *Meat Science*, *94*, 187–201. doi:10.1016/j.meatsci.2013.01.012

Sampels, S., Pickova, J., & Wiklund, E. (2004). Fatty acids, antioxidants and oxidation stability of processed reindeer meat. *Meat Science*, *67*, 523–32. doi:10.1016/j.meatsci.2003.12.006

Sandom, C. J., Hughes, J., & Macdonald, D. W. (2013). Rewilding the Scottish highlands: Do wild boar, *Sus scrofa*, use a suitable foraging strategy to be effective ecosystem engineers? *Restoration Ecology*, *21*, 336–343. doi:10.1111/j.1526-100X.2012.00903.x

Sañudo, C., Enser, M. E., Campo, M. M., Nute, G. R., María, G., Sierra, I., & Wood, J. D. (2000). Fatty acid composition and sensory characteristics of lamb carcasses from Britain and Spain. *Meat Science*, *54*, 339–346. doi:10.1016/S0309-1740(99)00108-4

Schaefer, T. (2004). Video monitoring of shrub-nests reveals nest predators. *Bird Study*, *51*, 170–177.

Schlageter, A., & Haag-Wackernagel, D. (2011). Effectiveness of solar blinkers as a means of crop protection from wild boar damage. *Crop Protection*, *30*, 1216–1222. doi:10.1016/j.cropro.2011.05.008

Schlageter, A., & Haag-Wackernagel, D. (2012a). A gustatory repellent for protection of agricultural land from wild boar damage: An investigation on effectiveness. *Journal of Agricultural Science*, *4*, 61–68. doi:10.5539/jas.v4n5p61

Schlageter, A., & Haag-Wackernagel, D. (2012b). Evaluation of an odor repellent for protecting crops from wild boar damage. *Journal of Pest Science*, *85*, 209–215. doi:10.1007/s10340-012-0415-4

Schley, L., Dufrêne, M., Krier, A., & Frantz, A. (2008). Patterns of crop damage by wild boar (*Sus scrofa*) in Luxembourg over a 10-year period. *European Journal of Wildlife Research*, *54*, 589–599. Retrieved from http://link.springer.com/article/10.1007/s10344-008-0183-x

Schumann, M., Schumann, B., Dickman, A, Watson, L. H., & Marker, L. (2006). Assessing the use of swing gates in game fences as a potential non-lethal predator exclusion technique. *South African Journal of Wildlife Research*, *36*, 173–181.

Sclater, W.L. (1900). *The Mammals of South Africa. Vol. 1*. London, England: R.H. Porter.

Sebranek, J. G., & Bacus, J. N. (2007). Cured meat products without direct addition of nitrate or nitrite: what are the issues? *Meat Science*, *77*, 136–147. doi:10.1016/j.meatsci.2007.03.025

Servanty, S., Gaillard, J. M., Ronchi, F., Focardi, S., Baubet, É., & Gimenez, O. (2011). Influence of harvesting pressure on demographic tactics: Implications for wildlife management. *Journal of Applied Ecology*, *48*, 835–843. doi:10.1111/j.1365-2664.2011.02017.x

Shaw, J.C.M. (1939). Growth changes and variation in warthog third molars and their palaeontological importance. *Transactions of the Royal Society of South Africa*, *27,* 51-94.

Shiferaw, H., Teketay, D., Nemomissa, S., & Assefa, F. (2004). Some biological characteristics that foster the invasion of *Prosopis juliflora* (Sw.) DC. at Middle Awash Rift Valley Area, north-eastern Ethiopia. *Journal of Arid Environments*, *58*, 135–154. doi:10.1016/j.jaridenv.2003.08.011

Shortridge, G. C. (1934). *The mammals of South West Africa*. London, England: W. Heinemann, Ltd.

Shortridge, G. C. (1942). Field notes on the first and second expeditions of the Cape Museums mammal survey of the Cape Province and descriptions of some new subgenera and species. *Annals of the South African Museum, 36*, 27–100.

Sifuna, N. (2010). Wildlife damage and its impact on public attitudes towards conservation: A comparative study of Kenya and Botswana, with particular reference to Kenya's Laikipia Region and Botswana's Okavango Delta Region. *Journal of Asian and African Studies*, *45*, 274–296. doi:10.1177/0021909610364776

Šimko, P. (2002). Determination of polycyclic aromatic hydrocarbons in smoked meat products and smoke flavouring food additives. *Journal of Chromatography B: Analytical Technologies in the Biomedical and Life Sciences*, *770*, 3–18. doi:10.1016/S0378-4347(01)00438-8

Sitters, J., Heitkönig, I. M. A., Holmgren, M., & Ojwang', G. S. O. (2009). Herded cattle and wild grazers partition water but share forage resources during dry years in East African savannas. *Biological Conservation*, *142*, 738–750. doi:10.1016/j.biocon.2008.12.001

Skead, J., Boshoff, A., Kerley, G. I. H., & Lloyd, P. (2007). *Historical incidence of the larger mammals in the broader Eastern Cape*. Port Elizabeth, South Africa: Centre for Conservation Ecology, Nelson Mandela Metropolitan University.

Skinner, J. D. & Chimimba, C. T. (2005). *The mammals of the southern African subregion*. (3rd ed.). Cambridge, England: Cambridge University Press.

Smit, Z. M. (2014). *The ecological planning of DoornKloof Nature Reserve, Northern Cape province*. MSc thesis, University of the Free State, Bloemfontein, South Africa

Smith, N., & Wilson, S. L. (2002). *Changing land use trends in the thicket biome : pastoralism to game farming*. Terrestrial Ecology Research Unit, University of Port Elizabeth, Port Elizabeth, South Africa.

Somers, M. J. (1992). The implications of social structure for the conservation and control of a warthog *Phacochoerus aethiopicus* population in the Andries Vosloo Kudu Reserve, Eastern Cape Province. MSc Thesis, University of Pretoria, Pretoria, South Africa.

Somers, M. J., & Penzhorn, B. L. (1992). Reproduction in a reintroduced warthog population in the eastern Cape Province. *South African Journal of Wildlife Research*, *22*, 57–57. Retrieved from http://www.sabinet.co.za/abstracts/wild/wild_v22_n3_a1.html

Somers, M. J., Penzhorn, B. L., & Rasa, A. E. (1994). Home range size, range use and dispersal of warthogs in the eastern Cape, South Africa. *Journal of African Zoology*, *108*, 361–373.

Somers, M. J., Rasa, O. A. E., & Penzhorn, B. L. (1995). Group structure and social behaviour of warthogs *Phacochoerus aethiopicus*. *Acta Theriologica*, *40*, 257–281.

Soriano, A., Cruz, B., Gómez, L., Mariscal, C., & García Ruiz, A. (2006). Proteolysis, physicochemical characteristics and free fatty acid composition of dry sausages made with deer (*Cervus elaphus*) or wild boar (*Sus scrofa*) meat: A preliminary study. *Food Chemistry*, *96*, 173–184. doi:10.1016/j.foodchem.2005.02.019

Sowls, L. K., & Phelps, R. J. (1966). Body temperatures of juvenile warthogs and bushpigs. *Journal of Mammalogy*, *47*, 134–137.

Spear, D., & Chown, S. L. (2009a). The extent and impacts of ungulate translocations : South Africa in a global context. *Biological Conservation*, *142,* 353–363. doi:10.1016/j.biocon.2008.10.031

Spear, D., & Chown, S. L. (2009b). Non-indigenous ungulates as a threat to biodiversity. *Journal of Zoology*, *279*, 1–17. doi:10.1111/j.1469-7998.2009.00604.x

Spencer, P. B. S., & Hampton, J. O. (2005). Illegal translocation and genetic structure of feral pigs in Western Australia. *Journal of Wildlife Management*, *69*, 377–384. doi:DOI: 10.2193/0022-541X(2005)069<0377:ITAGSO>2.0.CO;2

Springer, M. T., Bowman, J. L., & Vasilas, B. L. (2013). The effect of white-tailed deer browsing on wheat quality and yields in Delaware. *Wildlife Society Bulletin*, *37*, 155–161. doi:10.1002/wsb.242

Stevenson, J. M., Seman, D. L., & Littlejohn, R. P. (1992). Seasonal variation in venison quality of mature, farmed red deer stags in New Zealand. *Journal of Animal Science*, *70*, 1389–1396.

Stockton, S., Allombert, S., Gaston, A, & Martin, J. (2005). A natural experiment on the effects of high deer densities on the native flora of coastal temperate rain forests. *Biological Conservation*, *126*, 118–128. doi:10.1016/j.biocon.2005.06.006

Swanepoel, M., Leslie, A. J., & Hoffman, L. C. (2016). Farmers' perceptions of the extra-limital common warthog in the Northern Cape and Free State provinces, South Africa. *Wildlife Society Bulletin*. doi:10.1002/wsb.617.

Swanepoel, M., Schulze, E., & Cumming, D. (in press.). A conservation assessment of *Phacochoerus africanus*. In: M. F. Child, D. Raimondo, E. Do Linh San, L. Roxburgh & H. Davies-Mostert

(Eds.), *The Red List of Mammals of South Africa, Swaziland and Lesotho*. Pretoria, South Africa: South African National Biodiversity Institute and Endangered Wildlife Trust.

Szmańko, T., Górecka, J., Korzeniowska, M., Malicki, A., & Eeremenko, E. (2007). Comparison of chosen quality parameters of meat from wild boar and domestic pigs. *Polish Journal of Food and Nutrition Sciences*, *57*, 523–528.

Taylor, R. G., Labas, R., Smulders, F. J. M., & Wiklund, E. (2002). Ultrastructural changes during aging in M. *Longissimus thoracis* from moose and reindeer. *Meat Science*, *60*, 321–326. doi:10.1016/S0309-1740(01)00120-6

Taylor, W. A., Skinner, J. D., & Krecek, R. C. (2005). Seasonal body condition indices of mountain reedbuck (*Redunca fulvorufula*) in two areas of South African Highveld: the grassland and Karoo biomes. *South African Journal of Animal Sciences*, *35*, 19–29. doi:10.4314/sajas.v35i1.4045

Thackeray, J. F. (1979). An analysis of faunal remains from archaeological sites in southern South West Africa (Namibia). *The South African Archaeological Bulletin, 34*, 18–33

Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Niemann, S. M., & Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, *92*, 398–407. doi:10.1890/10-0126.1

Thurfjell, H., Spong, G., & Ericsson, G. (2013). Effects of hunting on wild boar *Sus scrofa* behaviour. *Wildlife Biology*, *19*, 87–93. doi:10.2981/12-027

Tierney, T. A., & Cushman, J. H. (2006). Temporal changes in native and exotic vegetation and soil characteristics following disturbances by feral pigs in a california grassland. *Biological Invasions*, *8*, 1073–1089. doi:10.1007/s10530-005-6829-7

Tobler, M. W., Cochard, R., & Edwards, P. J. (2003). The impact of cattle ranching on large-scale vegetation patterns in a coastal savanna in Tanzania. *Journal of Applied Ecology*, *40*, 430–444. doi:10.1046/j.1365-2664.2003.00816.x

Toldrá, F., & Reig, M. (2011). Innovations for healthier processed meats. *Trends in Food Science & Technology*, *22*, 517–522. doi:10.1016/j.tifs.2011.08.007

Treves, A., Wallace, R. B., Naughton-Treves, L., & Morales, A. (2006). Co-managing human–wildlife conflicts: A review. *Human Dimensions of Wildlife*, *11*, 383–396. doi:10.1080/10871200600984265

Treydte, A. C., Baumgartner, S., Heitkönig, I. M. A., Grant, C. C., & Getz, W. M. (2013). Herbaceous forage and selection patterns by ungulates across varying herbivore assemblages in a South African Savanna. *PloS One*, *8*, e82831. doi:10.1371/journal.pone.0082831

Treydte, A. C., Bernasconi, S. M., Kreuzer, M., & Edwards, P. J. (2006). Diet fo the common warthog (*Phacochoerus africanus*) on former cattle grounds in a Tanzanian Savanna. *Journal of Mammalogy*, *87*, 889–898.

Treydte, A., & Halsdorf, S. (2006). Habitat use of warthogs on a former cattle ranch in Tanzania. *The Journal of Wildlife Management*, *70*, 1285–1292. Retrieved from http://www.bioone.org/doi/abs/10.2193/0022-541X(2006)70%5B1285:HUOWOA%5D2.0.CO%3B2

Trollope, W. S. W. (1989). Veld burning as a management practice in livestock production. In J. E. Danckwerts & W. R. Teague (Eds.), *Veld management in the Eastern Cape* (pp. 67-73). Pretoria, South Africa: Government Printer.

Tuorila, H. M., Meiselman, H. L., Cardello, A. V, & Lesher, L. L. (1998). Effect of expectations and the definition of product category on the acceptance of unfamiliar foods. *Food Quality and Preference*, *9*, 421–430. doi:10.1016/S0950-3293(98)00012-3

Tweheyo, M., Tumusiime, D. M., Turyahabwe, N., Asiimwe, A., & Orikiriza, L. (2012). Wildlife damage and control methods around Lake Mburo National Park, Uganda. *International Journal of Pest Management*, *58*, 25–31. doi:10.1080/09670874.2011.641605

Valencak, T. G., Gamsjäger, L., Ohrnberger, S., Culbert, N. J., & Ruf, T. (2015). Healthy n-6/n-3 fatty acid composition from five European game meat species remains after cooking. *BMC Research Notes*, *8*, 273. doi:10.1186/s13104-015-1254-1

Valencak, T., & Gamsjäger, L. (2014). Lipids in tissues of wild game : Overall excellent fatty acid composition , even better in free- ranging individuals. In P. Paulsen, A. Bauer, & F. J. M. Smulders (Eds.), *Trends in Game Meat Hygiene* (pp. 335–344). Wageningen Academic Publishers. doi:10.3920/978-90-8686-238-2

Van der Merwe, M., Jooste, P. J., & Hoffman, L. C. (2012). Application of European standards for health and quality control of game meat on game ranches in South Africa. *Journal of the South African Veterinary Association*, *82*, 170–175. doi:10.4102/jsava.v82i3.63

Van der Merwe, P., & Saayman, M. (2003). Determining the economic value of game farm tourism. *Koedoe*, *46*, 103–112. doi:10.4102/koedoe.v46i2.59

Van der Plas, F., Zeinstra, P., Veldhuis, M., Fokkema, R., Tielens, E., Howison, R., & Olff, H. (2013). Responses of savanna lawn and bunch grasses to water limitation. *Plant Ecology*, *214*, 1157–1168.

Van der Wal, P. G., Bolink, A. H., & Merkus, G. S. M. (1988). Differences in quality characteristics of normal, PSE and DFD pork. *Meat Science*, *24*, 79–84. doi:10.1016/0309-1740(89)90009-0

Van Hoepen, E. C. N., & Van Hoepen, H. E. (1932). Vrystaatse wilde varke. *Paleontologiese Navorsing van die Nasionale Museum Bloemfontein, 2*, 39−62.

Van Hoepen, E. C. N. (1932). Voorlopige beskrywing van Vrystaatse soogdiere. *Paleontologiese Navorsing van die Nasionale Museum Bloemfontein, 2*, 63–65.

Van Schalkwyk, D. L., McMillin, K. W., Booyse, M., Witthuhn, R. C., & Hoffman, L. C. (2011). Physico-chemical, microbiological, textural and sensory attributes of matured game salami produced from springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*), kudu

(*Tragelaphus strepsiceros*) and zebra (*Equus burchelli*) harvested in Namibia. *Meat Science*, *88*, 36–44. doi:10.1016/j.meatsci.2010.11.028

Van Schalkwyk, D. L., McMillin, K. W., Witthuhn, R. C., & Hoffman, L. C. (2010). The contribution of wildlife to sustainable natural resource utilization in Namibia: A review. *Sustainability*, *2*, 3479–3499. doi:10.3390/su2113479

Van Vuren, D. H., & Wilcox, J. T. (2009). Wild pigs as predators in oak woodlands of California. *Journal of Mammalogy*, *90*, 114–118.

Van Zyl, L., & Ferreira, A. V. (2004). Physical and chemical carcass composition of springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus dorcas phillipsi*) and impala (*Aepyceros melampus*). *Small Ruminent Research*, *53*, 103–109. doi:10.1016/j.smallrumres.2003.08.017

Vanschoenwinkel, B., Waterkeyn, A., Nhiwatiwa, T., Pinceel, T., Spooren, E., Geerts, A., … Brendonck, L. (2011). Passive external transport of freshwater invertebrates by elephant and other mud-wallowing mammals in an African savannah habitat. *Freshwater Biology*, *56*, 1606–1619. doi:10.1111/j.1365-2427.2011.02600.x

Vazquez, D. P. (2002). Multiple effects of introduced mammalian herbivores in a temperate forest. *Biological Invasions*, *4*, 175–191. doi:10.1023/a:1020522923905

Veblen, K. E., & Young, T. P. (2010). Contrasting effects of cattle and wildlife on the vegetation development of a savanna landscape mosaic. *Journal of Ecology*, *98*, 993–1001. doi:10.1111/j.1365-2745.2010.01705.x

Vercammen, P., & Mason, D. R. (1993). *The warthogs* (P*hacochoerus africanus* and *P. aethiopicus*). .In W. L. R., Oliver (Ed.), *Pigs, peccaries, and hippos: status survey and conservation action plan* (pp. 110–133). Gland, Switzerland: IUCN/SSC Pigs and Peccaries Specialist Group. Retrieved from https://portals.iucn.org/library/efiles/edocs/1993-055.pdf.

Voeten, M. M., & Prins, H. H. T. (1999). Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia*, *120*, 287–294.

Volpelli, L. A., Valusso, R., Morgante, M., Pittia, P., & Piasentier, E. (2003). Meat quality in male fallow deer (*Dama dama*): effects of age and supplementary feeding. *Meat Science*, *65*, 555–562. doi:10.1016/S0309-1740(02)00248-6

Von la Chevallerie, M., Erasmus, J. M., Skinner, J. D., & Zyl, J. H. M. Van. (1971). A note on the carcass composition of the common eland (*Taurotragus oryx*). *Suid Afrika Tydskrif van Natuurnavorsing*, *1*, 129–131.

Waldram, M. S., Bond, W. J., & Stock, W. D. (2008). Ecological engineering by a mega-grazer: white rhino impacts on a South African Savanna. *Ecosystems*, *11*, 101–112. doi:10.1007/s10021-007-9109-9

Wambuguh, O. (2008). Human–urban wildlife interface: interactions around tilden regional park, San Francisco Bay Area, California. *Human Dimensions of Wildlife: An International Journal*, *13*, 71–72. doi:10.1080/10871200701812944

Wang, S., & Curtis, P. (2006). Farmer perceptions of crop damage by wildlife in Jigme Singye Wangchuck National Park, Bhutan. *Wildlife Society Bulletin*, *34*, 359–365. doi:10.2193/0091-7648(2006)34[359:fpocdb]2.0.co;2

Wardle, D. A., Barker, G. M., Yeates, G. W., Bonner, K. I., & Ghani, A. (2001). Introduced browsing mammals in New Zealand natural forests: Aboveground and belowground consequences. *Ecological Monographs*, *71*, 587–614. doi:10.1890/0012-9615(2001)071[0587:IBMINZ]2.0.CO;2

Warren, R. (2011). *A Spending Model for Biltong Hunters*. MSc thesis, North West University, Potchefstroom, South Africa.

Warren, Y., Buba, B., & Ross, C. (2007). Patterns of crop-raiding by wild and domestic animals near Gashaka Gumti National Park, Nigeria. *International Journal of Pest Management*, *53*, 207–216. doi:10.1080/09670870701288124

Warris, P. (2000). *Meat Science*. Oxon: CAB Publishing.

Webber, A. D. (2010). Assessing the impact of domestic goat (*Capra hircus*) damage upon maize yield in a Ugandan subsistence farming context. *International Journal of Pest Management*, *56*, 9–14. doi:10.1080/09670870902980826

Weise, F. J., Wessels, Q., Munro, S., & Solberg, M. (2014). Using artificial passageways to facilitate the movement of wildlife on Namibian farmland. *South African Journal of Wildlife, 44*, 161–166.

Weladji, R. B., & Tchamba, M. N. (2003). Conflict between people and protected areas within the Bénoué Wildlife Conservation Area, North Cameroon. *Oryx*, *37*, 72–79. doi:10.1017/S0030605303000140

Welander, J. (2000). Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting in a mosaic landscape. *Journal of Zoology*, *252*, 263–271. doi:10.1017/S0952836900009997

Wells, L. H. Cooke, H. B. S., Malan, B. D, Wells, L. H., & Cooke, H. B. S. (1942). The associated fauna and culture of Vlakkraal thermal Springs, O.F.S.; III, the faunal remains. *Transactions of the Royal Society of South Africa, 29*, 214-232.

Wentzel, J. J., Bothma, J. du P., & Van Rooyen, N. (1991). Characteristics of the herbaceous layer in preferred grazing areas of six herbivore species in the south-eastern Kryger National Park. *Koedoe*, *34*, 51–59.

West, B., & Parkhurst, J. (2002). Interactions between deer damage, deer density, and stakeholder attitudes in Virginia. *Wildlife Society Bulletin*, *30*, 139–147. Retrieved from http://www.jstor.org/stable/3784647

White, A. M. (2010). A pigheaded compromise: do competition and predation explain variation in warthog group size? *Behavioral Ecology*, *21*, 485–492. doi:10.1093/beheco/arq009

White, A. M., & Cameron, E. Z. (2009). Communal nesting is unrelated to burrow availability in the common warthog. *Animal Behaviour*, *77*, 87–94. doi:10.1016/j.anbehav.2008.08.030

White, P. C. L., & Lowe, P. (2008). Wild mammals and the human food chain. *Mammal Review*, *38*, 117–122. doi:10.1111/j.1365-2907.2008.00121.x

Wiklund, E., Andersson, A., Malmfors, G., & Lundström, K. (1996). Muscle glycogen levels and blood metabolites in reindeer (*Rangifer tarandus tarandus* L.) after transport and lairage. *Meat Science*, *42*, 133–144.

Wiklund, E., Dobbie, P., Stuart, a., & Littlejohn, R. P. (2010). Seasonal variation in red deer (*Cervus elaphus*) venison (M. *longissimus dorsi*) drip loss, calpain activity, colour and tenderness. *Meat Science*, *86*, 720–727. doi:10.1016/j.meatsci.2010.06.012

Wilby, A., Shachak, M., & Boeken, B. (2001). Integration of ecosystem engineering and trophic effects of herbivores. *Oikos*, *92*, 436–444. doi:10.1034/j.1600-0706.2001.920305.x

Wilfred, P. (2012). Trophy hunting and trophy size in Ugalla Game Reserve, western Tanzania. *Tanzania Journal of Science*, *38*, 111–122.

Williams, B. L., Holtfreter, R. W., Ditchkoff, S. S., & Grand, J. B. (2011). Trap style influences wild pig behavior and trapping success. *The Journal of Wildlife Management*, *75*, 432–436. doi:10.1002/jwmg.64

Wirthner, S., Frey, B., Busse, M. D., Schütz, M., & Risch, A. C. (2011). Effects of wild boar (*Sus scrofa* L.) rooting on the bacterial community structure in mixed-hardwood forest soils in Switzerland. *European Journal of Soil Biology*, *47*, 296–302. doi:10.1016/j.ejsobi.2011.07.003

Wirthner, S., Schütz, M., Page-Dumroese, D. S., Busse, M. D., Kirchner, J. W., & Risch, A. C. (2012). Do changes in soil properties after rooting by wild boars (*Sus scrofa)* affect understory vegetation in Swiss hardwood forests? *Canadian Journal of Forest Research*, *42*, 585–592. doi:10.1139/x2012-013

Wittmann, K., Vaske, J. J., Manfredo, M. J., & Zinn, H. C. (1998). Standards for lethal response to problem urban wildlife. *Human Dimensions of Wildlife*, *3*, 29–48. doi:10.1080/10871209809359137

Wood, J. D., Enser, M., Fisher, A. V, Nute, G. R., Sheard, P. R., Richardson, R. I., … Whittington, F. M. (2008). Fat deposition, fatty acid composition and meat quality: A review. *Meat Science*, *78*, 343–58. doi:10.1016/j.meatsci.2007.07.019

Wywialowski, A. P. (1994). Producers ' perceptions of agricultural wildlife-caused losses. *Wildlife Society Bulletin*, *22*, 370–382.

Yessoufou, K., Gere, J., Daru, B. H., & Van der Bank, M. (2014). Differences in evolutionary history translate into differences in invasion success of alien mammals in South Africa. *Ecology and Evolution*, *4*, 2115–2123. doi:10.1002/ece3.1031

Yoganand, K., & Owen-Smith, N. (2014). Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography*, *37*, 1–14. doi:10.1111/ecog.00534

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Chapter 3

The pests and pathogens of the common warthog in South Africa: A review

Abstract

Wildlife is the primary source of animal and zoonotic diseases and of major importance to the agricultural and public health sector since they cause production and financial losses, including mortalities among livestock animals, while zoonotic diseases cause debilitating illnesses or death in humans. As the global wildlife-livestock-human interface is expanding and growing more complex, the possibility of pathogen transmission among these compartments is expected to increase. Hunting and game meat consumption are important activities among many societies, with wild species often being translocated and introduced by humans for these purposes. However, intentionally introduced species may become naturalized and disperse within the surrounding area, providing pathways for potential disease transmission among hosts. The common warthog (*Phacochoerus africanus*) has been extra-limitally introduced to reserves and ranches across the country including the former range of the extinct Cape warthog (*P. aethiopicus*). The species are popular for recreational and trophy hunting and have traditionally been hunted and consumed as game meat, similarly to the introduced feral pig. Warthogs are associated with a number of important animal and zoonotic diseases, such as African Swine Fever and bovine tuberculosis, with the potential to act as a wild reservoir. This raises serious concerns as the species are not restricted by standard fencing and move freely among natural and agricultural lands, with their distribution range expanding across South Africa. This review summarizes the pests and pathogen associated with common warthogs, current disease control measures in South Africa and the implications for human consumption of warthog meat.

1 Introduction

1.1Wildlife diseases

Wildlife may carry or be susceptible to a range of different diseases which affects domestic livestock or humans (Daszak et al., 2000). Wildlife diseases are of major importance to the agricultural and public health sector since they cause production and financial losses, including mortalities among livestock animals, while zoonotic diseases cause debilitating illnesses or death in humans (Kruse et al., 2004, Dhama et al., 2013). Additionally, livestock may harbor exotic diseases that are transmissible to wildlife, who in turn act as carriers or spillover hosts, thereby maintaining the disease in the environment despite vaccination of livestock (Siembieda et al., 2011, Rhyan & Spraker, 2010, Miller et al., 2013). This bi-directional nature of animal diseases has important implications as the livestock-wildlife interface continues to expand and become more complex, with changing types of land use becoming more intertwined (Bengis et al., 2002).

Of all the known human pathogens 61% are zoonoses, as are 75% of emerging diseases (Taylor et al., 2001). Human zoonotic infections occur mainly through handling of infected animals or carcasses and consumption of infected meat (Ahl, Nganwa, & Wilson, 2002). Hunting and game meat consumption is an important activity among many societies and it is therefore necessary to educate hunters on the risks associated with wildlife species, while the role of scientists is to detect and recognize diseases of significance. Hoffman and Cawthorn (2012) provide an extensive overview of the consumption of meat from wild animals on a global scale, with reference to the dependence of African peoples on the meat as protein source, sourced from wild or farmed populations. The continent is host to a number of important zoonotic diseases which are highly infectious to humans and multiple animal species. For example, trichinosis and echinococcosis are intestinal parasites of humans obtained through ingesting infected, undercooked meat, of which game meat is a common source (Pozio, 2007). Both may cause debilitating diseases in humans and death in severe cases with important economic implications regarding public health and livestock production. The bacterium responsible for anthrax, *Bacillus anthracis*, has historically been responsible for devastating epidemics among domestic and wild animals in sub-Saharan Africa, with an outbreak in 1923 causing the death of an estimated 30 000 to 60 000 animals in South Africa (Sterne, 1967 in Hugh-Jones & De Vos, 2002). The disease is endemic to parts of southern Africa with both animal and human infections reported during the most recent outbreaks in 2013 and 2014 in Namibia, Zimbabwe and Lesotho (National Institute for Communicable Diseases [NICD], 2014). Human infections occur from contact with infected meat, mucosal membranes and damaged skin, inhalation of spores or ingestion of infected meat; the case fatality rate is however low (< 1%).

Rabies is another disease that can infect all mammalian species, with the canine strain responsible for the majority of infections among animals and humans. The domestic dog (*Canis familiaris*), yellow mongoose (*Cynictis penicillata*), black-backed jackal (*Canis mesomelas*) and bat-eared fox (*Otocyon megalotis*) are considered the dominant maintenance hosts and readily transmit the virus interspecies, while an interherbivorial outbreak among greater kudu (*Tragelaphus strepsiceros*) in Namibia in the 1970's resulted in the loss of 30 000-50 000 animals (Bishop et al., 2003). Slaughtering and consuming raw meat from rabid animals have been implicated in human cases of rabies, but not for ingestion of cooked meat (Bishop et al., 2010).

The main diseases targeted by the Disease Reference Group on Zoonosis and Marginalized Infectious Diseases (DRG6) (World Health Organization [WHO], 2012) are presented in Table 1. All of these diseases have been recorded to infect humans in southern Africa while certain groups, including persons in animal-related occupations, hunters and poor and marginalized communities, are more vulnerable to contracting and spreading animal diseases. According to the Food and Agricultural Organization of the United Nations (FAO, 2013), livestock health is the weakest link in the global human health chain, and controlling animal and agricultural product movement is the most effective preventative measure for introducing and spreading animal diseases to a country and within its borders.

Table 4: The zoonotic diseases targeted by the Group on Zoonosis and Marginalized Infectious Diseases (DRG6) (Source: World Health Organization [WHO] 2012).

Helminth infections	Protozoan infections	Viral infections	Bacterial infections
Taeniasis/Cysticercosis	Cryptosporidiosis	Rabies	Brucellosis
Echinococcosis	Toxoplasmosis		Certain enteric bacterial pathogens
Food-borne trematodiases			Bovine Tuberculosis
Zoonotic schistosomiasis			Anthrax

Poor and marginalized communities in particular are disproportionately affected by zoonotic-and-vector borne diseases due to their dependency on livestock and bushmeat (Bengis et al., 2002, Molyneux et al., 2011). Early detection of potential zoonosis and dissemination of this knowledge to these groups could help limit zoonotic infections, and contribute to improving public health among these communities. Anthropogenic activities such as transportation and introduction of species, provision of feeding stations and occurrence of feral animals have been identified as major facilitators of disease outbreaks among livestock and wildlife (Dobson & Foufopolous, 2001). In southern Africa, all of these are facets of the wildlife ranching industry which poses a unique situation for animal and human health. Additionally, feeding stations, including supplementary feeding or mineral licks, and permanent water points are typical features of livestock farms and intensive game farming operations, which may serve as an important source of disease spread as wild and domestic animals tend to aggregate around these points (Bengis et al., 2002).

In some cases, intentionally introduced species are able to become naturalized and disperse within the surrounding area (Fraser, Cone & Woodford, 2000, Forsyth & Duncan, 2001), posing a disease risk as feral or free-ranging species. Feral pigs (*Sus scrofa*), for example, have been introduced onto every continent except Antarctica and are heavily persecuted for damage reprisal, but are also considered a popular game animal for sport hunting and meat production, the main reason they were originally introduced (Bengsen, Gentle, Mitchell, Pearson & Saunders, 2014). The species are associated with, and may act as wild reservoir of economically devastating diseases such as African Swine fever and bovine tuberculosis, and humans have been infected with hepatitis E virus (HEV), *Trichinella* spp. and *Toxoplasma gondii* from ingestion of infected meat (Meng, Lindsay & Sriranganathan, 2009). Subsequently, there has been increasing concern regarding disease outbreaks among introduced/translocated populations as the contact between feral-and-domestic-animals and humans increases, and Kock, Woodford and Rossiter (2010) provide a global review of the risks and implications of species translocations/introductions and wildlife disease.

1.2 Background to game ranching

The production and utilization of wild animals as a food and revenue resource has become an increasingly popular industry among many southern African countries. Game ranching (also referred to as game farming), is a production system where wild animals are managed extensively or intensively on private or communal land, exclusively or in conjunction with other agricultural practices, including livestock rearing (Cousins et al., 2008). The establishment and success of the industry is attributed to the change in wildlife protection policies and private land-and wildlife-ownership during the 1960's and 70's which encouraged wildlife protection and utilization on state-owned and private reserves (Luxmoore, 1985, Benson, 1991). The shift from livestock to wildlife based production was further encouraged by observations that indigenous wildlife are better adapted to the harsh conditions of marginal lands across the African continent, the high diversity of wildlife and the availability of land unsuitable for livestock production (Child et al., 2012, Lindsey et al., 2013).

It is estimated that there are currently about >9 000 game farms covering 205 000 km^2 operating in South Africa (Lindsey et al., 2013). The game farming industry generates revenue through eco-tourism, recreational (biltong)-and-trophy hunting, live trade and sales, taxidermy and meat production (Van der Merwe & Saayman 2003, Cloete et al., 2007), whilst providing jobs and other socio-economic opportunities for local communities (Department of Agriculture, Forestry and Fisheries [DAFF], 2013a). Wildlife species that are valued as game animals are regularly introduced and/or translocated to farms and reserves as part of the game farming industry in South Africa. Species introductions are driven by the demand of tourists and hunters for certain species and a greater diversity of species, which is associated with increased economic activity (Barnes & De Jager, 1996, Castley et al., 2001). The practice appears to be confounded by the country's natural species richness and the lack of a national framework which governs the game farming industry (Spear & Chown, 2009, Cousins et al., 2010). This, together with increased stocking densities of domestic and wild animals on the same or adjacent properties (Ocaido et al., 1996), has raised legitimate concerns regarding the prevalence of animal diseases among wild and domestic animals (Bekker et al., 2012). Recently, the Department of Environmental Affairs has embarked on developing a national framework for the norms and standards of translocation of indigenous Species (Department of Environmental Affairs [DEA], 2015).

1.3 Warthog as an extra-limital species

The common warthog (*Phacochoerus africanus*) was introduced extra-limitally to provincial reserves in the Northern Cape, Free State and Eastern Cape provinces of South Africa (Figure 1), initially as part of re-wildling efforts of a warthog species (Cape warthog, *P. aethiopicus*) thought to have gone extinct (Penzhorn, 1971). In South Africa, their known natural range includes the upper north-eastern parts of the country including the Limpopo, Mpumalanga and marginal parts of the Kwa-Zulu Natal/Mozambique border (Rautenbach, 1982, Skinner & Chimimba, 2005, Skead et al., 2007). Inland, warthogs also occur in the northern parts of North West province and the border of the Northern Cape and Botswana (Figure 1). These introductions were followed by introductions on private game farms and reserves across the country for eco-tourism and hunting purposes (Nyafu, 2009). Multiple introduction events coupled with a high reproduction rate has allowed warthogs to greatly expand their range and inhabit areas where they were historically absent.

Warthogs are a species not contained within the borders of a property by standard wire or wire mesh fencing and can be considered a free-roaming species in South Africa. All three provinces (Northern Cape, Free State and Eastern Cape) where these introductions occurred are important agricultural producers utilizing the majority of land for farming purposes, and warthog presence has been positively associated with the occurrence of pastoral farms (Bamford et al., 2014). The Northern Cape covers an area of 363 389 km^2 of which 81% is utilized for agricultural purposes. The major agricultural activity is stock farming, including cattle (*Bos taurus*), sheep (*Ovis aries*), and goat (*Capra hircus*), while crop farming comprises 2% of the total land use due to the aridity of the area. The Free State province covers 129 825 km^2 with agriculture accounting for 90% of the land use, of which about 57% is used for livestock farming and 33% for crop production. The Eastern Cape covers 170 616 km^2 of which 86% is used for farming (DAFF, 2013b). Game farming has become a major form of agricultural land-use in all three provinces, with game farms covering 48 520 km^2 (13.4% of total area) of the Northern Cape and 8 816 km^2 (5.2% total area) of the Eastern Cape.

Warthogs are a known agricultural pest and have become a managerial problem in traditional agricultural settings. Some farmers currently employ a shoot-on-sight strategy to control populations and mitigate negative impacts, while game farmers exploit the species for financial gain through hunting and tourism. The species have traditionally been hunted and consume as bushmeat by rural communities (Martin et al., 2012), but is also a popular species for recreational and trophy hunters. In 2009 a total of 2049 warthogs were officially recorded as being hunted by international trophy hunters in South Africa which increased to 3 849 in 2013, making warthogs the 2nd most often trophy hunted in South Africa (Professional Hunters Association of South Africa (Professional Hunters Association of South Africa [PHASA], 2014). These numbers however do not represent all the warthogs hunted in the country as it is expected that the majority of recreational and damage control hunting remain unreported.

Warthogs currently inhabit both private and public lands on which major agricultural activities are practiced in South Africa. Despite being associated with a number of important animal and zoonotic diseases, there has been almost no attention given to the prevalence and risk of disease among free-ranging warthog populations in South Africa. Warthogs are considered the major host of the *Ornithodoros* tick species which is responsible for the transmission and spread of African Swine fever (ASF) in domestic pigs (Penrith & Vosloo, 2009). They have also been experimentally infected with the virus responsible for Classical Swine fever (CSF), and able to spread the disease to other warthogs (Everett et al., 2011). While the ASF and CSF viruses are unrelated, both cause devastating diseases in domestic pigs with severe economic consequences. Considering the potential implications the distribution and movement of free-ranging warthogs could have for livestock and game animal production, and for the consumption of warthog meat by humans, this review aims to summarize the most important diseases that have been reported for warthogs in sub-Saharan Africa.

Figure 7: The known natural distribution range of the common warthog (yellow shading), with the initial points of extra-limital introductions indicated in yellow circles, and the original source of these introduced warthogs indicated by a yellow star (Map modified from source: IUCN, 2013).

2 Diseases associated with warthogs potentially transmissible to animals and humans

The most important diseases associated with warthog that are potentially transmissible to animals and humans are presented in Table 2 and 3, respectively. Each disease is briefly discussed regarding the current state of knowledge on warthogs, the measures taken towards disease prevention and spread and the future avenues for research. A short section at the end provides an overview of other potential warthog diseases that could pose a future risk for animal and human health, but on which very limited knowledge is available.

2.1 African Swine fever

African Swine fever (ASF) is arguably the most important disease associated with warthogs in Africa. Warthogs are considered to be the original host and carrier of the ASF virus, a unique DNA arbovirus indigenous to Africa. This highly contagious disease is of major concern for domestic pig production as it has a 100% mortality rate in pigs and its prevalence in sub-Saharan Africa continues to greatly impede the development of piggeries for pork production (Penrith & Vosloo, 2009). Following infection, pigs develop hemorrhagic fever and succumb within 5–15 days. Warthogs and argasid ticks (or tampans), *Ornithodoros porcinus* and *O. moubata*, are the natural hosts that maintain the ASF virus in an ancient sylvatic cycle in eastern and southern Africa (Penrith et al., 2004). The argasid ticks are mainly found in warthog burrows, but occasionally occur on adult warthogs where they are transported to grazing and farmed areas, coming into contact with domestic pigs (Gallardo et al., 2011). Neonate warthogs become infected when bitten by infected ticks in burrows and develop detectable viremia for 2-3 weeks but do not develop the disease. Although animals stay infected for life, no detectable viremias have been found in older animals (Thomson, 1985). Therefore, ticks only become infected with ASF virus when feeding on neonate warthogs with elevated blood virus levels due to their limited immune systems.

Although Thomson (1985) found that all diagnosed cases of ASF among domestic pigs were in countries where warthogs occur, the co-distribution of warthogs and *Ornithodoros* spp. does not imply the existence of ASF in an area (Jori & Bastos, 2009). Other than the sylvatic cycle, the virus is also maintained in a cycle between domestic pigs and *O. porcus* in pig shelters, and among domestic pigs without an apparent wild Suidae host or tampan vector (Costard et al., 2009, Jori et al., 2013) (Figure 2). The movement of infected pigs and pig products has been considered the major route of ASF transmission in African countries where warthogs are absent (Penrith & Vosloo, 2009); all of the last outbreaks in South Africa since 1994 were caused by the movement of infected animals or animal products.

In South Africa the disease is limited to the Limpopo and parts of the Kwa-Zulu Natal and Mpumalanga provinces by the ASF control zone (Figure 3), where transmission and infection is primarily prevented by monitoring the movement of wild and domestic pigs and their products from and within the controlled zone. The most recent outbreak in 2011 in Gauteng was effectively contained within the infected pig population before it could spread (Penrith, 2013), which emphasizes the importance of maintaining strict biosecurity measures to protect against infection and spread. Infections outside of the control zone are treated by stamping out, where infected and in-contact herds are quarantined and slaughtered, since there is no vaccine or treatment for ASF. South Africa has been heralded as an example of how an ASF free-zone can be established and maintained within an endemic area (Costard et al., 2009). However, the illegal transportation of wild suid carcasses by humans and hunters remains a concern for spreading ASF in South Africa and across national boundaries, since the ASFV can remain infectious for extended periods of time in meat and meat products (Penrith & Vosloo, 2009). South Africa is also unique regarding the diversity of pig production enterprises; ranging from free ranging rural herds on communal lands, to large scale commercial production systems, which increases the complexity of continued surveillance and protection programs.

There is a paucity of information regarding the current prevalence and occurrence of ASF among *Ornithodoros* ticks in South Africa. Madder et al. (2013) indicated that the distribution range of the tampan follows that of the warthogs' distribution, which was historically limited to the more northern and eastern parts of South Africa (refer to Figure 1 for *P. africanus* and Figure 6 for *O. moubata*), and there is limited evidence that the distribution range of the tampan vector is changing in some parts of

South Africa (Penrith & Vosloo, 2009). Arnotet al. (2009) and Boshoff et al. (2014) found no ASF viruses among *O. porcinus* ticks collected from warthog burrows in a game reserve within the ASF control zone and in Swaziland (respectively) which is adjacent to the ASF control zone. The findings of Arnot et al. (2009) are especially significant since ASF virus was detected, albeit at low prevalence (0.06%), in sampled tick populations in 1978, and since the warthog population had grown by 59% and tick infestation rate of warthog burrows had increased by 27%. The authors suggested that either the virus had disappeared from the area or that it was extremely localized. The prevalence and occurrence of ASF in *Ornithodoros* spp., and distribution of tampans and their hosts, are important areas for future research especially as the common warthog continues to expand its distribution in South Africa.

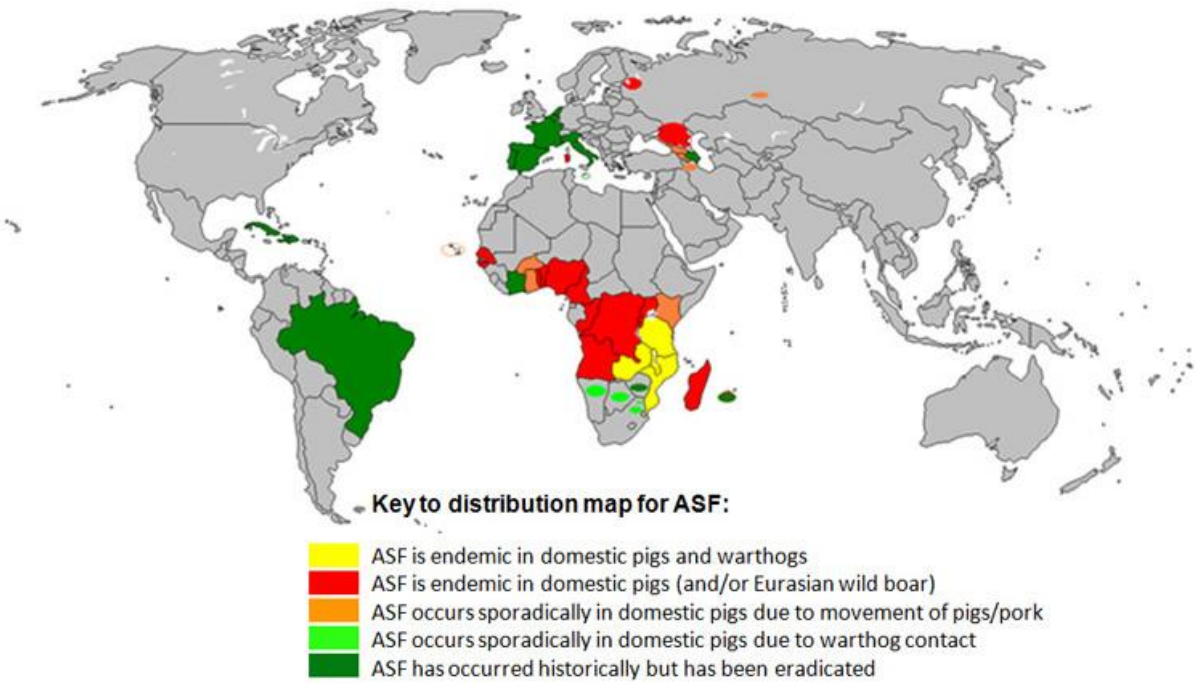

Figure 8: The global distribution of African Swine fever and the cycles of maintenance (Source: Penrith et al., 2004).

2.2 Classical Swine fever

Classical Swine Fever (CSF) is considered the most important disease of swine globally. It has been responsible for devastating economic losses across continents and in countries with notable pig production activities. The disease is caused by a small RNA virus which produces similar clinical symptoms and lesions to ASF in domestic pigs although the viruses are unrelated (Moennig et al., 2003). It is a highly infectious hemorrhagic disease which causes severe morbidity and mortality in domestic pigs in its acute form, but can also manifest in a subacute or chronic form (Moennig, 2000). This is attributed to strain variability, with moderately virulent strains responsible for chronic and protracted illness, while the associated immunosuppressive effect often results in mortalities from secondary infections. The disease is circulated and maintained among wild and domestic pigs through ortonasal transmission or contamination of the environment, most notably pigswill (Edwards et al., 2000). Infected pigs begin to shed the virus during the incubation period when no physical symptoms have started to develop, and no combination of physical signs, symptoms or lesions can be used to predictably detect a suspected outbreak (Penrith et al., 2011)

It was successfully eradicated in South Africa after its initial introduction in the early 1900's, but was reintroduced in 2005 causing an outbreak among piggeries in the Eastern Cape. Large-scale pig slaughters (stamping out) and the implementation of strict regulations governing the transportation of live domestic and wild pigs and their products from the infected area has effectively brought the disease under control, and while there is still a control zone enforced (Figure 3), the disease is considered as eradicated in South Africa (Penrith et al., 2011, Penrith, 2013). Currently no live pig or pig product (domestic and wild) may be moved from the CSF control zone, and special permits are to be obtained if pig products are to be moved from or through the zone. The Eastern Cape province is host to large populations of rural pigs, warthogs and bushpigs (*Potamochoerus larvatus*), and there have been concerns that the disease might become established in wild suid populations, since experimental infection and intra-species transmission of CSF have been shown for both warthogs and bushpigs (Everett et al., 2011). Penrith et al. (2011) suggested that warthogs might not play the same role in CSF epidemiology as with ASF, considering the ancient sylvatic cycle between warthogs and ASF virus tick vectors. However, future studies should aim to determine whether these wild suids may play a role in CSF epidemiology in South Africa.

Despite the existence of an effective vaccine, many countries including South Africa have abstained from vaccination as the difference between vaccinated and naturally infected serologically positive animals cannot be detected. Therefore the continued implementation of strict biosecurity measures is required to keep South African herds free from infections.

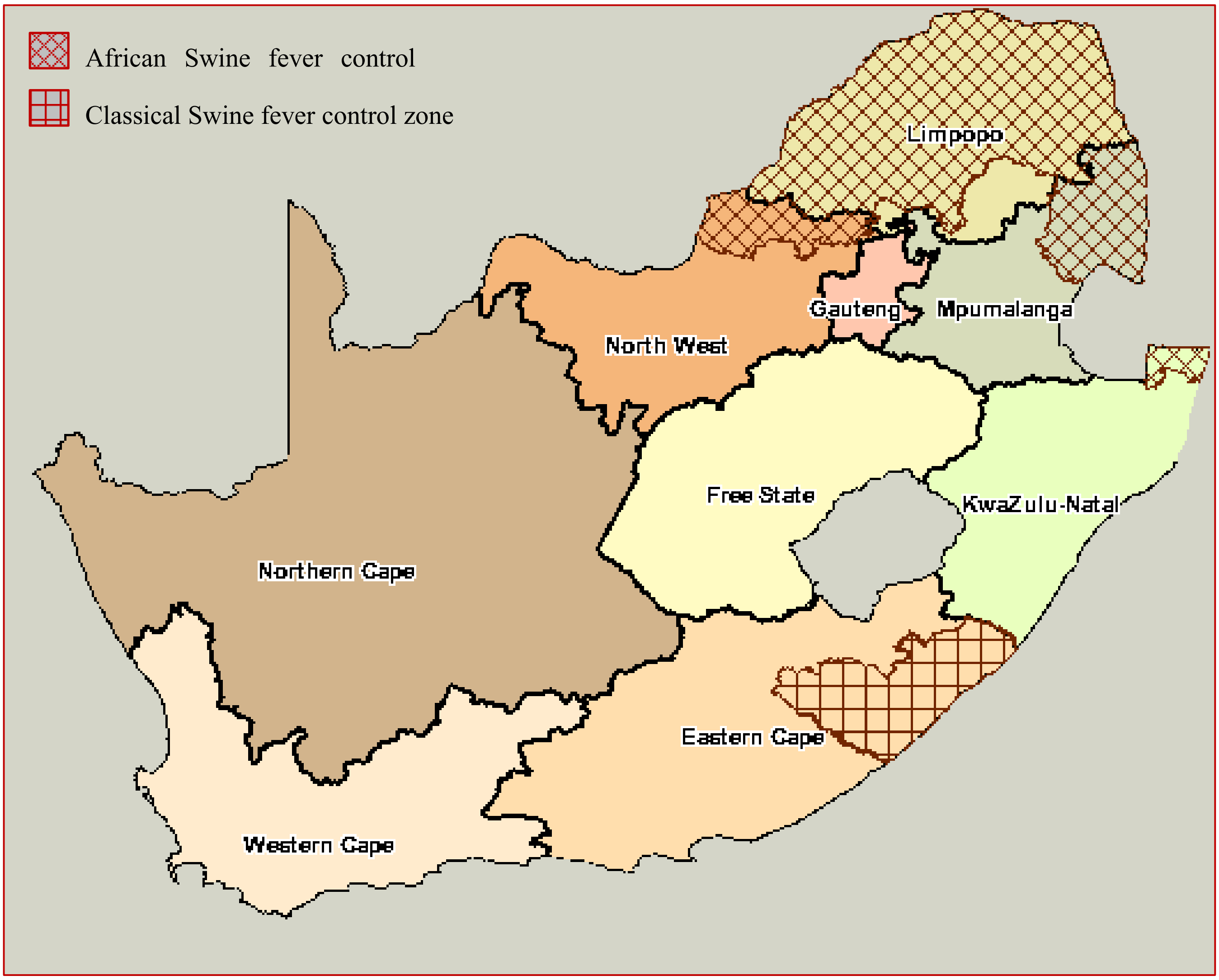

Figure 9: The African and Classical Swine fever control zones in South Africa (Source: http://www.agis.agric.za).

2.3 Rift Valley Fever

Rift Valley Fever (RVF) is caused by an arbovirus of the family *Bunyaviridae*, genus *Phlebovirus*. Endemic to sub-Saharan Africa, the virus was first diagnosed during an outbreak among infected sheep in the greater Kenyan Rift Valley in 1931 (Pepin et al., 2010). The virus is carried and transmitted primarily by mosquitos from the *Aedes* and *Culex* geneses which infect animals through their saliva during feeding. The virus requires a vertebrate host in order to replicate and spreads by infecting other mosquitos that feed on infected animals. Since host animals only remain viremic for a couple of days, the invertebrate host may play a pivotal role in maintaining virus circulation among seasons. Periodic outbreaks (5–15 years) occur after heavy rains or floods where the accumulated surface water on shallow soil provides an ideal breeding ground for mosquito vectors (LaBeaud et al., 2010). RVF causes a high rate of abortions and perinatal mortalities in pregnant ruminant animals, fetal malformation, and subclinical-to-fatal febrile illness in animals and humans.

There have been localized outbreaks of Rift Valley fever in South Africa among domestic and wild animals since the 1950's (Pienaar & Thomson, 2013). Outbreaks have been widespread but are increasingly frequent in central, summer rainfall regions, one of the regions warthogs have been introduced to (Figure 4). During the 2010 epidemic, signs of RVF in a number of indigenous and exotic wildlife were reported for the first time. These included springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus dorcas dorcas*), bontebok (*D. dorcas phillipsi*), waterbok (*Kobus ellipsiprymnus*), African buffalo (*Syncerus caffer*), sable (*Hippotragus niger*), greater kudu (*T. strepsiceros*), nyala (*Tragelaphus angasii*), gemsbok (*Oryx gazella*), fallow deer (*Cervus dama*), llama (*Lama glama*), alpaca (*Lama pacos*), Asian buffalo (*Bubalus bubalis*) and ibex (*Capra ibex*) (Pienaar & Thompson, 2013). Although warthogs are not considered a wild host, Evans et al. (2008) discovered RVF antibodies in two warthogs in Kenya, and high levels of seropositivity have been found among populations also in Kenya, indicating that warthogs might be among the wild ungulates that play a role in the epidemiology of the virus (Britch et al., 2013). Other ungulates with seropositivity in this study were waterbok, impala (*Aepyceros melampus*), African buffalo, common eland (*Taurotragus oryx*), giraffe (*Giraffa camelopardalis*), gerenuk (*Litocranius walleri*), and also domestic camel (*Camelus dromedaruis*).

There are still many gaps in understanding the epidemiology of RVF virus in the environment and the role of wild animals in maintaining and spreading the disease (Evans et al., 2008, Pienaar & Thompson, 2013). It has been suggested that wild animals, and certain domestic herds, maintain the virus through low-level circulation between periodic outbreaks, without the population manifesting any clinical symptoms (Pepin et al., 2010). The possibility of domestic or wild animals acting as spillover hosts in areas with a history of RVF outbreaks still requires investigation (Magwedere et al., 2012). Britch et al. (2013) suggested targeted serological surveillance among both livestock and wild ungulates to better understand the epidemiology of the virus, and possibly predict future outbreaks. Surveillance should be conducted before, during and after outbreaks as indicated by the authors to hopefully further elucidate the interepidemic maintenance and cycles of RVF.

If wild animals, and free-ranging warthogs, are potential maintenance host of the virus, continued vaccination of livestock in areas prone to RVF outbreaks could be the best method for effective disease management, while Oberem and Oberem (2011) suggested the application of pyrethroids on valuable game animals to prevent mosquito bites. Human infections with RVF are primarily through contact with infected dead animal tissue, including meat and mucosal membranes. There were a total of 302 laboratory confirmed cases of RVF in humans between 2008 and 2011 in South Africa of which 60% were farmers and farm labourers on animal farms (Archer et al., 2013). During this time period, 25 infections were fatal while contact with an infected warthog carcass (not confirmed) was suspected to be the source of infection in one fatality in 2008 (Paweska, 2014). This case fatality rate of 8% was higher than the estimated 0.5-2% among human cases in Africa and Arabian Peninsula given by Pepin et al. (2010). There is no treatment for RFV but prevention is possible through livestock and human vaccination and mosquito control. Educational efforts should aim to improve farmer and hunter knowledge on the risks associated with handling potentially infected animal tissue. Considering the long term persistence of the virus within mosquito vectors, the industry is yet to develop long term vaccines for humans and animals (LaBeaud, 2011).

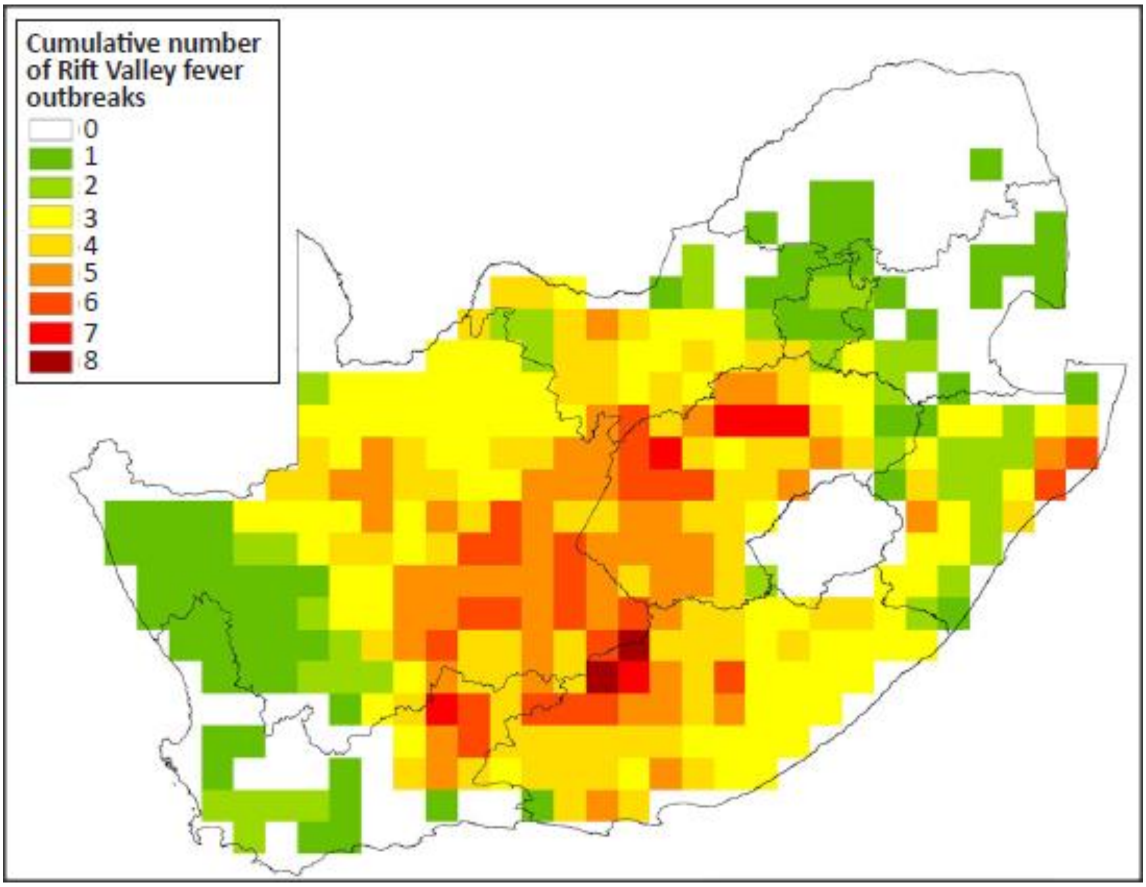

Figure 10: The cumulative number of seasons during which Rift Valley Fever outbreaks occurred in South Africa from 1950-2011 (Source: Pienaar & Thompson, 2013).

2.4 Foot-and-mouth disease

Foot-and-mouth disease (FMD) is recognized as one of the most important livestock and game animal diseases globally. It is caused by a highly infectious aphtovirus of the family *Picornaviridae*, and although not fatal, greatly affects agricultural production including plant and plant product production (Thomson et al., 2003). The virus is epitheliotrophic with infected animals developing fever, lameness and vesicular lesions in the mouth and on the snout, feet and teats, which affects eating/feeding. It can cause myocarditis and death in young calves, lambs and piglets, and in some wild ungulate species (Bengis & Erasmus, 1988, Arzt et al., 2011). Endemic to many sub-Saharan African countries, transmission occurs through direct contact with infected animals, or mechanical transfer through contaminated animal feed, machinery, humans, animal and plant products, fomites or by airborne aerosols (Sellers & Gloster, 2008).

Essentially all members of *Artiodactyla* are susceptible to the virus but species and breeds may vary with degree of susceptibility, clinical manifestation of the disease and ability to infect (Arzt et al., 2011). Regarding domestic species, cattle (*Bos taurus*) appear to be the main reservoir of FMD viruses globally, while in South Africa, the Cape buffalo (*Syncerus caffer*) is the main host and long-term carrier of the South African Territories 1–3 (SAT 1–3) serotypes of FMD virus (Hedger, 1972,Thomson et al., 2003). The disease is maintained among buffalo populations in Kruger National Park (KNP) with periodic spillovers to other wildlife species, but wildlife has to date not been implicated in maintaining the disease independently.

Warthogs are reportedly highly susceptible to SAT 1 strains with reports of acute illness and death (Bengis & Erasmus, 1988). The species have experimentally been infected with SAT 2 and were able to infect other warthogs through contact, but did not become carriers (Hedger et al., 1972). This was also demonstrated for bushpigs, but there has been no evidence to date that either of these wild Suidae can become persistently infected. The SAT 2 serotype has been responsible for the majority of outbreaks among cattle and wildlife in and around the KNP (Dyason, 2010), affecting bushbuck (*Tragelaphus scriptus*), nyala (*Tragelaphus angasii*), sable antelope (*Hippotragus equinus*) and roan antelope (*Hippotragus niger*). Kudu and impala have been implicated in transmitting FMD from infected buffalo populations to cattle (Hargreaves et al., 2004).

The FMD control zone encompasses the KNP and northern borders of Kwa Zulu Natal with the three OIE control zones as indicated in Figure 5. The control zone monitors the movement of live cloven hoofed animals and their products from within the infected and buffer zones and the control measures are defined by the Veterinary Procedural Notice for Foot and Mouth Disease Control in South Africa. The fence is however subjected to extensive damage from primarily elephants (*Loxodonta africana*) and humans, which allows wildlife to enter surrounding farmlands and rural communities, and excluded cattle to enter the reserve (Jori et al., 2011). Warthogs were among the species observed to permeate fences and move between the reserve and surrounding areas. This impedes the effectiveness of veterinary fencing to separate domestic and wild animals and increases the likelihood of infectious diseases such as FMD being transmitted to naïve herds.

The last outbreak in South Africa outside of the control zone was in 2011, and resulted in the country losing its 'OIE FMD free without vaccination' status. In June 2012, the Directorate: Animal Health (in terms of Regulation 20 of the Animal Diseases Act, Act 35 of 1984) prohibited the movement of any live cloven hoofed animal from the FMD control zone in South Africa or from any area outside the country that is not recognized as free from FMD by the OIE. Strict implementation of these measures resulted in the country's 'FMD free without vaccination' status being partly restored in February 2014 and wholly restored in February 2015 (DAFF, 2015). Considering the massive economic implications FMD can have on countries with favorable livestock trade opportunities, it is a priority for South Africa to survey and maintain this status.

Although FMD is not considered a zoonosis, there have been recorded cases of human infection in the United Kingdom but these are extremely rare even among people that work in close contact with infected animals (Mayor, 2001, Prempeh et al., 2001).

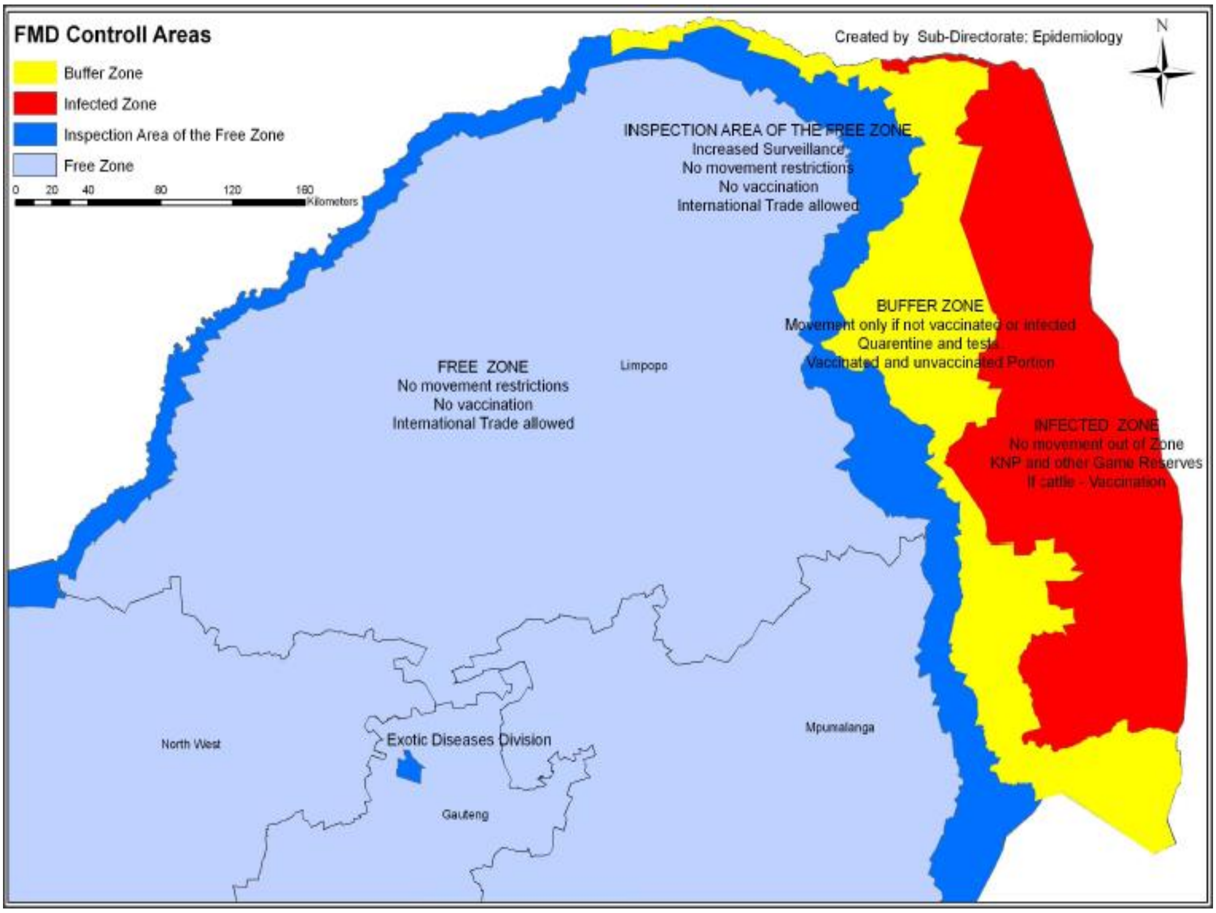

Figure 11: The Foot and Mouth Disease control zone in South Africa (Source: http://www.nda.agric.za).

2.5 Bovine tuberculosis

The bacterium *Mycobacterium bovis,* the causative agent of bovine tuberculosis (bTB), is exotic to South Africa and was introduced through infected cattle imported by colonial settlers in the 1880's (De Vos et al., 2001). The first confirmed case of infected wildlife was in greater kudu in the Eastern Cape in 1929, but the first widespread outbreaks occurred among buffalo populations in the KNP during the 1960's. Strong circumstantial evidence suggest buffalo became infected from sharing pasture with infected cattle, as it is now known that transmission occurs through either respiratory or alimentary (sharing nourishment resources) pathways (Michel et al., 2006). The typical clinical signs of bTB are weight loss, dyspnea and swollen peripheral lymph nodes, with lesions forming on the lungs and lymph nodes of the head (Renwick et al., 2007), but it may take years before infected individuals develop clinical symptoms (De Vos et al., 2001).

Domestic cattle are considered the main reservoir of the disease while Cape buffalo are the most important maintenance host in South Africa. The disease has also been detected among a number of South African wildlife species (Table 4). Lions (*Panthera leo)* are especially vulnerable to the disease since buffalo are one of their preferred prey, while cheetahs (*Acinonyx jubates*) and leopards (*Panthera pardus*) possibly contract the disease from scavenging lion-buffalo-kills (Michel et al., 2006). Warthogs and greater kudu appear to be important long-term maintenance hosts at high densities (De Lisle et al., 2002, Kalema-Zikusoka et al., 2005).

In South Africa the disease is monitored and controlled by the Bovine Tuberculosis Scheme (Regulation 1953 of 30 September 1988), and the control area around the KNP prevents free movement of wildlife species between infected and disease-free zones (DAFF, 2013c). Control measures require that in confirmed cases of bTB all animals are quarantined and slaughtered, while buffalo populations in the KNP and Hluhluwe-Umfolozi Game Reserve are subjected to surveillance and monitoring programs. However, recent studies have found that the spatial distribution of the disease is expanding in southern Africa despite these control measures. Hlokwe et al. (2014) found bTB among cattle and wildlife in provinces that were previously considered free from infection, including Mpumalanga, Limpopo, KwaZulu–Natal, Free State and North West provinces. The study also confirmed *M. bovis* infection in blue wildebeest (*Connochaetes taurinus*) for the first time. De Garine-Wichatitsky et al. (2010) found limited evidence that the disease is spreading northward from the KNP possibly through transmission of buffalo or an unidentified wildlife species to local cattle herds. Spatial expansion of the disease poses an important threat to both animal and human populations in southern African countries, especially considering the prevalence of HIV among human populations in this region (http://www.unaids.org/). Humans with HIV are increasingly at risk of contracting bTB due to the immune-suppressive effect of the virus (Grange, 2001). It remains unknown to what degree the prevalence of bTB among wild and domestic animals are responsible for human bTB infections. It is important to educated humans on the associated risks of contracting bTB from infected carcasses, and the relevant safety measures required in order to protect themselves from infection.

One of the greatest challenges of managing bTB is that the majority of infected wildlife shows no clinical symptoms, which limits the ability to detect the disease before infection becomes evident (De Lisle et al. 2002). Furthermore, the spread and maintenance of bTB among free-ranging animals is confounded by high densities of maintenance and spillover hosts, and focal concentration of animals around supplemental feeding sites and artificial water points (De Lisle et al., 2002). These are typical conditions present on a large number game farms in South Africa. The practice of species translocation and introduction for game ranching or conservation purposes has also been implicated in spreading the disease in South Africa (Hlokwe et al., 2014). Hlokwe et al. (2014) suggested that wildlife should be screened for bTB before translocation or introduction as most ranched wildlife species have been infected, or in contact with infected species at some point. Current research on bTB control promotes increased screening efforts of domestic and wild animal populations, decreasing population densities of wildlife populations, the development and application of an efficient vaccine and improved diagnostics

(Fitzgerald & Kaneene, 2013). Another potential strategy to increase surveillance efforts could focus on educating hunters and farmers on how to inspect for bTB post-mortem in hunted wildlife, especially where hunting is a common activity.

Table 4: South African wildlife species in which *Mycobacterium bovis* infection has been confirmed to date.

Species
African buffalo (*Syncerus caffer*)
Blue wildebeest *(Connochaetes taurinus)*
Bushbuck *(Tragelaphus scriptus)*
Bushpig *(Potamochoerus porcus)*
Chacma baboon (*Papio ursinus*)
Cheetah *(Acinonyx jubatus)*
Common genet (*Genetta genetta*)
Eland *(Taurotragus oryx)*
Greater kudu *(Tragelaphus strepsiceros)*
Grey duiker *(Sylvicapra grimmia)*
Honey badger *(Mellivora capensis)*
Impala *(Aepyceros melampus)*
Large spotted genet (*Genetta tigrina*)
Lechwe *(Kobus leche)*
Leopard *(Panthera pardus)*
Lion *(Panthera leo)*
Nyala *(Tragelaphus angasii)*
Rhinoceros (Unidentified spp.)
Spotted hyaena (*Crocuta crocuta*)
Warthog *(Phacochoerus africanus)*
Waterbuck *(Kobus ellipsiprymnus)*

Adapted from Michel et al., 2006.

2.6 Echinococcosis

A number of domestic and wild animals act as intermediate hosts for larvae of the dog (*Canis lupus familiaris*) tapeworm (*Echinococcus granulosus*) which causes the zoonotic parasitic disease echinococcosis (hydatidosis) (Otero-Abad & Torgerson, 2013). Adult tapeworms infest the intestine of the definitive carnivore host (domestic dog, black backed jackals [*Canis mesomelas*], cape silver fox [*Vulpes chama*], spotted hyena, and lion) and produce oocysts, which are excreted into the environment and ingested by the intermediate herbivore host. Intermediate herbivore hosts include Burchell's zebra (*Equus quagga*), Cape buffalo, greater kudu, hippopotamus (*Hippopotamus amphibius*) and impala (Bengis & Veary, 1997). The larvae occur as hydatid cysts on the liver or in the lungs of the intermediate host and are usually well tolerated, unless they develop on the brain, kidneys or heart, become large enough to damage adjacent organs, or burst, which causes anaphylactic shock and death (World Organisation for Animal Health and World Health Organization [WHO/OIE], 2002).

Hüttner et al. (2009) found *E. granulosus* and *E. felidis* in warthog samples from the Queen Elizabeth National Park in Uganda, and suggested that they could be intermediate hosts to both species. The prevalence of *Echinococcus* among warthog populations in South Africa appears low; hydatid cysts were recovered from the lungs of only one of six sampled warthogs in the Limpopo province (Van Wyk & Boomker, 2011), one of 28 sampled warthogs in a reserve adjacent to the KNP (Boomker et al., 1991) and eight from 52 warthogs sampled within the KNP (Horak et al., 1988). Low prevalence among intermediate wildlife hosts is likely the result of the absence of larger predators, considering the importance of predator-prey relationship in sylvatic transmission of certain *E. granulosus* strains (Jenkins & MacPherson, 2003).

Seven strains of *Echinococcus* have been identified as infectious to humans, with the sheep strain (G1) of *E. granulosus* responsible for the majority of human cases. Wahlers et al. (2013) reported on the rising number of echinococcosis cases among humans in South Africa as recorded by the National Health Laboratory Service (NHLS), but since cystic echinococcosis has a long latency period it is difficult to determine the actual prevalence of the disease. Interestingly, Wahlers et al. (2012) found that a high prevalence of the disease in animals does not necessarily correspond with a high prevalence in the human population in contact with infected animals and vice versa. Studies on the epidemiology of the disease is lacking in southern Africa in general and requires further research to determine its prevalence among animal hosts in the region, and the main routes of human infections (Wahlers, et al., 2012).

2.7 Trypanosomiasis

Warthogs are one of the most important maintenance hosts of tsetse flies (*Glossina* spp.), the vector of *Trypanosoma* spp., which causes trypanosomiasis in humans or nagana disease in cattle (Claxton et al., 1992). While the parasite posed a serious threat to livestock production during initial colonization of South Africa in the late 19th century, the rinderpest epidemic which raged through the African continent from 1887–1897, had the unexpected benefit of also drastically reducing the southern African distribution range of the main vector *G. mortisans mortisans*. Together with intensive DDT use on farms and reserves, two tsetse fly species (*G. mortisans mortisans* and *G. pallidipes*) were eventually eradicated, and the impact of the parasite on livestock is limited to parts of Kwa Zulu Natal where small tsetse fly populations of *G. austeni* and *G. brevipalpis* still persist (Gillingwater et al., 2010).

2.8 Trichinosis

Trichinella spp. are internal parasites of wild carnivores and pigs, where the adult worm infests the intestines and the larvae occur as cysts in the muscle tissue. Domestic and wild animals and humans can contract *Trichinella* infections when ingesting raw or undercooked meat infested with *Trichinella* cysts, but only humans develop clinical trichinosis. The ensuing infection in humans can manifest as an acute and chronic disease with debilitation symptoms and cause death in severe cases. There has been a significant global re-emergence of trichinosis post 1970, which together with anthropogenic factors, is greatly exasperated by the maintenance and transmission of the parasites within a sylvatic cycle between wildlife reservoirs and domestic animals (Pozio, 2007).

There are currently seven species and three related genotypes recognized globally, but only *T. nelsoni* and T8, genotype of *T. britovi*, have been found among certain large carnivore and small omnivore species in KNP (Marucci et al., 2009). Warthogs infected with *T. nelsoni* have been reported from Tanzania (Trichinella Reference Centre [ITRC] www.iss.it/site/Trichinella), and there have been outbreaks of trichinosis in Senegal, Algeria, Ethiopia and Kenya after ingesting improperly prepared warthog and/or bushpig (*P. larvatus*) meat (Mukaratirwa et al., 2013). Although freezing and cooking meat to a specific internal temperature is considered effective methods to kill the parasite (Gamble et al., 2000), it has been shown that the causative agent of trichinosis in West Africa, *T. britovi*, is more resistant to freezing (Pozio et al., 2006). Dupouy-Camet et al. (2009) reported on three cases of human infections after consuming warthog ham of which the meat had been deep frozen for several weeks before processing. Although not confirmed, *T. britovi* was the suspected infectious agent.

While studies on the prevalence of *Trichinella* infections among animals and humans are generally lacking in southern Africa, there has been no reports of *Trichinella* infections in domestic animals or humans in South Africa, Zimbabwe, Namibia or Mozambique (Pozio, 2007), and none among wild animals in South Africa outside of KNP. It should therefore be a continued effort to monitor for *Trichinella* infections in animals to prevent the introduction of the parasite elsewhere in South Africa.

2.9 Rabies

All mammalian species can contract rabies while carnivores are the major hosts of the canine strain, RABV, which accounts for the majority of humans and animals infections. The disease remains in circulation primarily among stray dogs and smaller wild carnivores in South Africa, with the highest prevalence amongst carnivores in Kwa-Zulu Natal. In South Africa, there were 12 confirmed cases of human rabies and 834 animal cases in 2012, of which 212 were among domestic animals and 114 among wildlife (WHO, 2013). While warthogs can become infected and transmit rabies, there were only two confirmed cases of infected warthogs between 1990 and 2009 in Namibia (Magwedere et al., 2012), but no confirmed warthog cases have been reported in South Africa since 1990 (Bishop et al., 2003).

2.10 Schistosomiasis

Schistosoma spp., commonly called bloodflukes, are prevalent among a number of wildlife species in sub-Saharan Africa, who act as intermediate or definitive hosts to different species (Horak et al., 1988, Weyher et al., 2010). Wild and domestic animals may develop chronic or acute schistosomiasis depending on the specific species involved, while human infections are caused primarily by *S. haematobium, S. mansoni*, and *S. japonicum*. The ensuing infection in humans is commonly called bilharzia. It is one of the most prevalent but also most neglected tropical diseases globally among humans (WHO, 2010). *Schistosoma* eggs are excreted in the feces or urine of infected animals or humans into freshwater sources where they hatch into miracidia, infecting freshwater snails and after multiplying through a number of cycles, are released as free-swimming larvae called cercariae. Freshwater snails are the primary reservoir of parasitic worms. Animals and humans become infected through contact with infected water or by accidentally ingesting the eggs. Cercariae penetrate the skin of animals and humans and develop into schistosomula, which are transported by the lymph or blood system to internal organs or the urinary tract (WHO, 2014). The South African species, *S. mansoni* and *S. haematobium*, are found in parts of Mpumalanga, Limpopo, Kwa-Zulu Natal and Eastern Cape provinces. Horak et al. (1988) found a *Schistosoma* spp. in a warthog in KNP, but there is very little known as to whether the species may play a role in the parasite's epidemiology in Africa.

2.11 Other diseases

Two probable cases of anthrax were reported for warthogs in the Serengeti Ecosystem, Tanzania, between 1996 and 2009 (Lembo et al., 2011) and it has been suggested that members of the Suidae family are more resilient to the bacterium (Hugh-Jones & De Vos, 2002). There have been no reports of *Brucella* or *Clostridium botulinum* in warthogs, both important diseases for cattle and game animal production. Warthogs have been suggested as possible intermediate hosts of the pork tapeworm, *Taenia solium,* but evidence that the species plays a significant role in its epidemiology among suids and humans is lacking. *Taenia solium* is one of the most important zoonotic parasites globally as humans are both an intermediate and definitive host and become infected by consuming raw or undercooked meat infected with cysticerci, which is the larval form of the parasite (Sciutto et al., 2000). Domestic pigs and dogs are considered the main intermediate hosts (Ito et al., 2002). Considering its importance as zoonosis, research into the possibility of warthogs as potential intermediate hosts is required for South Africa and the Africa continent as a whole.

It is possible for warthogs as warm-blooded vertebrates to become infected with *Toxoplasma gondii*, but no cases in wild suids have been reported in Africa yet (Riemann et al., 1975, Hove and Davey 1999, Hove & Mukaratirwa, 2005). The coccidian parasite, *Neospora caninum,* previously misclassified as *T. gondii* due to structural similarities, is responsible for causing neosporosis in wild and domestic animals. The disease causes abortions and neonatal mortalities in livestock and certain wildlife species. Lion, cheetah and white rhinoceros (*Ceratotherium simus)* have tested positive for seroprevalence in South Africa (Cheadle et al., 1999, Williams et al., 2002). Antibodies to *N. caninum* have been found in warthogs in Kenya but the sample size was small, making it difficult to extrapolate about the prevalence of the parasite in warthogs (Ferroglio et al., 2003). This study also found positive seroprevalence in zebra (*Equus quagga*), common eland, African buffalo, Thomson gazelle (*Eudorcas thomsonii*), impala, spotted hyena and in free-ranging cheetah. There is in general a lack of information regarding the prevalence of this parasite among domestic and wild animals in Africa, while no cases of human infections have been reported (Dubey et al., 2007).

Two species of *sarcocystis* have been described for warthogs, *Sarcocystis dubeyella* and *S. phacochoeri*; the latter forms visible cysts of about 4 mm (Stolte et al., 1998). *Sarcocystis* are protozoan parasites which occur as cysts in the cardiac and skeletal muscle of infected animals and humans. Livestock and wild animals rarely show clinical symptoms but cases of acute sarcocystosis have occurred among cattle in South Africa (Van Der Lugt et al., 1994). While acute sarcocystosis may cause debilitating effects including abortion in animals, the most important impact however is the resulting financial losses as animal carcasses with visible cysts are likely to be declared unfit for human consumption. There is little known about the distribution *Sarcocystis* spp. among warthogs and other wildlife in southern Africa, and their occurrence outside the KNP is yet to be determined.

It has recently been established that wild boars may serve as a source of hepatitis E infections in humans, through consumption of the meat from animals infected with the virus (HEV) (Meng et al., 2009). While it has been suggested that warthogs may carry the disease in South Africa and act as zoonotic agents (S. Korsman, pers.comm), there has been no evidence found of this to date, while the authors are aware, and have contributed, towards ongoing research efforts to further illuminate on this possibility in the country.

Table 2: Diseases associated with warthogs of importance to livestock and game animals.

Disease	Causative agent	Vector/Host	Animals affected	Impact on production	Status in South Africa	Reference
<u>Viruses</u>						
African Swine fever	African Swine fever virus	*Ornithodoros porcinus* and *O. moubata* ticks, warthogs	Domestic pigs, bushpigs	Mortalities	Confined to Limpopo and parts of Kwa-Zulu Natal and Mpumalanga by ASF control zone	Penrith & Vosloo, 2009
Classical Swine fever	Classical Swine fever virus	Domestic pigs	Domestic pigs, bushpigs	Mortalities	Confined to Eastern Cape province by Classical Swine Fever control zone	Penrith et al., 2011
Rift Valley Fever	Phlebovirus	Mosquitoes *Aedes* and *Culex* spp.	Domestic and wild animals	High rates of abortion, neonatalities and mortality in young	Occasional regional outbreaks	Britch et al., 2013
Foot and mouth disease	Foot and mouth disease virus, family *Picornaviridae*	African buffalo, cattle	Domestic and wild hoofed animals	Severe production losses	Confined to the Kruger National Park (KNP) and parts of Limpopo and Mpumalanga provinces by FMD control zone	Bengis & Erasmus, 1988
<u>Bacteria</u>						
Bovine tuberculosis	*Mycobacterium bovis*	Notably cattle and buffalo	Domestic and wild animals	Animal production losses, mortalities	Confined to the bTB control area around Kruger National Park	De Lisle et al., 2002
Parasites						

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Disease	Causative agent	Vector/Host	Animals affected	Impact on production	Status in South Africa	Reference
Echinococusis	*Echinococcus granulosus*	Carnivores	Domestic and wild herbivores	Animal production losses, mortalities	Low prevalence	Horak et al., 1988
Nanaga disease	*Trypanosoma* spp.	Tsetse fly *Glossina* spp., cattle, elephants, wild suids	Domestic and wild ruminants	Animal production losses, mortalities	Low prevalence, isolated to parts of Kwa-Zulu Natal	Claxton et al. ,1992

Table 3: Diseases associated with warthogs of importance for public health.

Disease	Causative agent	Human infections	Source of infection	Status in South Africa	Reference
Viruses					
Rift Valley Fever	Phlebovirus	Potentially fatal	Handling of infected carcasses	Occasional regional outbreaks	Paweska, 2014
Rabies	*Rhabdoviridae* (canine strain)	Fatal if untreated	Exchanging mucosal material with rabid animal through bites, open wounds	High prevalence in Eastern Cape and Kwa-Zulu Natal	WHO, 2013
Parasites					
Echinococcosis (hydatidosis)	*Echinococcus granulosus*	Can cause debilitating illness, death	Consumption of raw or undercooked pork or warthog meat	Low prevalence among domestic or wild swine	Wahlers et al., 2013
Trichinosis	*Trichinella* spp.	Intestinal infestation, can cause death	Consumption of raw or undercooked meat from infected animals	No cases reported for domestic animals and humans in South Africa	Mukaratirwa et al., 2013
Bilharzia	*Schistosoma* spp.	Causes debilitating illness	Organism penetrates skin in freshwater, accidental ingestion of eggs	A re-emerging neglected tropical disease in Eastern Cape, Kwa-Zulu Natal, Limpopo and Mpumalanga	Horak et al., 1988

3 Internal parasites

The helminths that have been recorded for common warthogs in South Africa and Namibia are listed in Table 5. The most common helminth species recorded by several authors include *Oesophagostomum spp., Probstmayria vivipara, Murshidia humata, Physocephalus sexalatus* and *Ascaris phacochoeri* (Horak et al., 1983, Horak et al., 1988, Boomker et al., 1991, Van Wyk & Boomker, 2011). Wyk and Boomker (2011) found a 100% prevalence of *O. mwanzae* and *P. vivipara* in warthog populations sampled from the Limpopo province, with warthogs having a mean helminth burden of 2228 (excluding *P. vivipara*) compared to impalas (592), kudus and blue wildebeest (407), black wildebeest (*Connochaetus gnou*) (588), gemsbok (184) and waterbuck (2150). The mean burden of *P. vivipara* was 501 000. This nematode is considered a parasite of horses and may occur in large numbers, although no clinical symptoms of infection are observed. It has been suggested that more exploratory feeders have higher and more diverse burdens of internal parasites (J. Boomker, pers. comm.). Horak et al. (1988) also recovered nymphs of the pentastomid *Linguatula nuttalli* from warthogs in KNP. The nymphs are known to infect the livers of kudu and wildebeest without causing any significant damage. Humans can become infected by certain *Linguatula* pentastomids by ingestion of undercooked viscera of infected animals, acting as intermediate hosts, and developing visceral pentastomiasis (Tappe & Büttner, 2009), although no cases of human pentastomiasis caused by *L. nuttalli* have been recorded.

Table 5: Helminths species of warthogs in South Africa and Namibia.

Helminth species	Life stage present	Location	Record
Trematodes			
Gastrodiscus aegyptiacus Railliet 1893	A	KNP	Horak et al., 1988
Schistosoma spp.	A	KNP	Horak et al., 1988
Cestodes			
Echinococcus spp.	Cysts	KNP	Horak et al., 1988
	L	Hoedespruit NR	Boomker et al., 1991
	Cysts	Limpopo	Van Wyk& Boomker, 2011
Paramoniezia phacochoeri Baylis 1927	A	Limpopo	Van Wyk & Boomker, 2011
Moniezia/ Paramoniezia	A (Scolices)	Namibia	Horak et al., 1983
	A (Scolices)	KNP	Horak et al., 1988
	A	Hoedespruit NR	Boomker et al., 1991
Taenia crocutae	Cysts	KNP	Horak et al., 1988
Taenia hyaenae larvae	Cysts	KNP	Horak et al., 1988
Taenia regis larvae	Cysts	KNP	Horak et al., 1988
	L	Hoedespruit NR	Boomker et al., 1991
Nematodes			
Ascaris phacochoeri Gedoelst 1916	3^{rd}, 4^{th}, A	KNP	Horak et al., 1988
	A	Hoedespruit NR	Boomker et al., 1991
Ascaris spp.	4^{th}	Namibia	Horak et al., 1983
Cooperia hungi Mönnig 1931	A	Hoedespruit NR	Boomker et al., 1991

Helminth species	Life stage present	Location	Record
	A	Limpopo	Van Wyk & Boomker, 2011
Cooperia spp.	A	Namibia	Horak et al., 1983
Impalaia nudicollis Mönnig 1931	4th A	Namibia	Horak et al., 1983
Impalaia tuberculate Mönnig 1923	4th, A	KNP	Horak et al., 1988
	A	Hoedespruit NR	Boomker et al., 1991
	A	Limpopo	Van Wyk & Boomker 2011
Microfilaria spp. (senzu Neitz 1931)		Zululand	Neitz, 1931
Microfilaria		KNP	Palmieri et al., 1985
Murshidia hamata Daubney 1923	A	KNP	Horak et al., 1988
	L, A	Hoedespruit NR	Boomker et al., 1991
Murshidia pugnicaudata (Leiper 1909)	A	KNP	Horak et al., 1988
	L, A	Hoedespruit NR	Boomker et al., 1991
	A	Limpopo	Van Wyk & Boomker, 2011
Murshidia spp.	4th	KNP	Horak et al., 1988
	L	Hoedespruit NR	Boomker et al., 1991
Odontogeton phacochoeri Allgrén 1921		Natal	Allgrén, 1921*
Oesophagostomum mocambiquei Ortlepp 1964	A	KNP	Horak et al., 1988
	L, A	Hoedespruit NR	Boomker et al., 1991
	A	Limpopo	Van Wyk & Boomker, 2011
Oesophagostomum mpwapwae	A	Namibia	Horak et al., 1983
Oesophagostomum mwanzae	A	Namibia	Horak et al., 1983
	A	KNP	Horak et al., 1988

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Helminth species	Life stage present	Location	Record
	L, A	Hoedespruit NR	Boomker et al., 1991
	A	Limpopo	Van Wyk & Boomker, 2011
Oesophagostomum roubaudi Daubney 1926	A	Namibia	Horak et al., 1983
Oesophagostomum spp.	4^{th}	Namibia	Horak et al., 1983
	4th	KNP	Horak et al., 1988
	L	Hoedespruit NR	Boomker et al., 1991
Physocephalus sexalatus Diesing 1861	3^{rd}, 4^{th}, A	Namibia	Horak et al., 1983
	3^{rd}, 4^{th}, A	KNP	Horak et al., 1988
	L, A	Hoedespruit NR	Boomker et al., 1991
	A	Limpopo	Van Wyk & Boomker, 2011
Probstmayria vivipara Ransom 1911	4^{th}	Namibia	Horak et al., 1983
	4^{th}	KNP	Horak et al., 1988
	L, A	Hoedespruit NR	Boomker et al., 1991
	A	Limpopo	Van Wyk & Boomker, 2011
Strongyloides spp.	A	KNP	Horak et al., 1988
Trichostrongylus falculatus Ransom 1911	A	KNP	Horak et al., 1988
Trichostrongylus deflextus Boomker & Reinecke 1989	A	Hoedespruit NR	Boomker et al., 1991
Trichostrongylus thomasi Mönnig 1932	A	KNP	Horak et al., 1988
	A	Hoedespruit NR	Boomker et al., 1991
Trichostrongylus colubriformis	A	Namibia	Horak et al., 1983
Trichostrongylus instabilis	A	KNP	Horak et al., 1988
Trichostrongylus spp.	A	Hoedespruit NR	Boomker et al., 1991

Helminth species	Life stage present	Location	Record
Trichuris spp.	4th stage	KNP	Horak et al., 1988
Pentastomes			
Linguatula nuttalli	N	KNP	Horak et al., 1988

Adapted from Boomker et al., (1991).
*After Round (1968).
A = Adults
N = Nymphs
L = Larvae

4 External parasites

Ecto-parasites that have been recovered from warthogs in southern Africa are presented in Table 6, and the distribution of the most important vectors of diseases in Figure 6. Among these, *Rhipicephalus (Boophilus) decoloratus, R. everesti everesti, H. rufipes* and *R. simus* have been recorded to carry and transmit *Anaplasma marginale,* the causative agent of Bovine anaplasmosis (De Waal, 2000). Mutshembele et al. (2014) found that *R. decoloratus* and *R. eversti eversti* are the main species involved in *A. marginale* transmission in South Africa, and the prevalence of *A. marginale* is high across the country except in the arid North Cape province. Horak et al. (1988) considered *R. decoloratus* and *R. evertsi eversti* (and *H. truncatum*) accidental parasites of warthogs and a reflection of their wide-spread occurrence, rather than host preference.

The tick *Rhipicephalus simus* is responsible for transmitting the parasite *Babesia trautmanni* which causes Porcine babesiosis in domestic pigs. Warthogs are a wild host of the piroplasm and one of the preferred hosts of the tick species but develop no clinical symptoms (Stewart et al., 1992). The distribution of *R. simus*, as shown in Figure 6, does not include the drier central region of South Africa, where Matthee et al. (2013, Addendum A) found the tick among introduced warthog populations. This suggests that the tick was introduced with the introduced warthog populations. There has been a general low prevalence of *Babesia* parasites in the drier central parts of South Africa (Mtshali and Mtshali, 2014), but the introduction of *R. simus* outside its natural range might increase the distribution range of *B. trautmanni*. The tick typically has a low load of parasitism on individual animals, which reduces the risk of transmission and infection between wild and domestic suids, but high loads have been recovered from a healthy warthog (221), a sick lion (713) and a sick leopard (521) (Walker et al., 2000). Certain *Babesia* spp. are known to infect humans but the condition is rarely severe, except in cases of immunocompromised or asplenic individuals (Gorenflot et al., 1998, Gray et al., 2010).

Warthogs are considered to be the major host of the tick *Amblyomma hebraeum* (Horak et al., 1988, Gallivan & Surgeoner, 1995) the tick-vector of *Ehrlichia ruminantium* (formerly *Cowdria ruminantium*) the causative agent of heartwater in wild and domestic ruminants. It is not known whether warthogs act as wild reservoirs for the bacterium, while suspected wild reservoir species include blesbok, black wildebeest (*Connochaetes gnou*), common eland, giraffe (*Giraffa camelopardalis*), greater kudu, African buffalo and sable antelope (Peter et al., 1997, 2002). *A. hebraeum* is also the principle vector of *Rickettsia africae*, the bacterium responsible for most human tick bite fever cases in humans in southern Africa, which appears to be more common among non-African travelers than local habitants (Jensenius et al., 2003).

Tick infestations themselves may cause sickness or physical damage. The toxins in the saliva of certain strains of *H. truncatum* and *R. everesti everesti* (and also *R. eversti mimeticus*) cause sweating sickness in cattle and paralysis in lambs, respectively (Oberem & Oberem, 2011). Severe infestations of *R. appendiculatus* on an animal's ear may lead to loss of the ear.

Table 6: The ecto-parasites of warthog in South Africa and Namibia.

Ecto-parasite	Life stages present	Area	Reference
<u>Fleas</u>			
Echidnophaga larina	-	Hoedespruit	Boomker et al., 1991
	A	KNP	Horak et al., 1988
	A	Namibia	Horak et al., 1983
	-	Free State	Matthee et al., 2013
Moeopsylla sjoestedti	-	Hoedespruit	Boomker et al., 1991
	A	KNP	Horak et al., 1988
<u>Lice</u>			
Haematopinus phacochoeri	N A	Hoedespruit	Boomker et al., 1991
	N A	KNP	Horak et al., 1988
	N A	Namibia	Horak et al., 1983
	-	Free State	Matthee et al., 2013
<u>Ixodid ticks</u>			
Amblyomma hebraeum	L N A	Hoedespruit	Boomker et al., 1991
	L N A	Swaziland	Gallivan & Surgeoner, 1995
Amblyomma marmoreum	L	Hoedespruit	Boomker et al., 1991
Hyalomma truncatum	L	Hoedespruit	Boomker et al., 1991
	A	KNP	Horak et al., 1988
	A	Namibia	Horak et al., 1983
	-	Free State	Matthee et al., 2013
Hyalomma marginatum rufipes	A	Namibia	Horak et al., 1983
Rhipicephalus simus	A	Hoedespruit	Boomker et al., 1991
	A	KNP	Horak et al., 1988
	A	Namibia	Horak et al., 1983
	A	Swaziland	Gallivan & Surgeoner, 1995
	-	Free State	Matthee et al., 2013
Rhipicephalus (Boophilus) decoloratus	L	Hoedespruit	Boomker et al., 1991
	A N L	KNP	Horak et al., 1988
Rhipicephalus appendiculatus	L	Hoedespruit	Boomker et al., 1991

	N	KNP	Horak et al., 1988
	A N L	Swaziland	Gallivan & Surgeoner, 1995
Rhipicephalus everesti everesti	N L	Hoedespruit	Boomker et al., 1991
	N L	KNP	Horak et al., 1988
Rhipicephalus everesti mimeticus	A N	Namibia	Horak et al., 1983
Rhipicephalus zambeziensis	A N	Hoedespruit	Boomker et al., 1991
	N	KNP	Horak et al., 1988
Rhipicephalus longiceps	A	Namibia	Horak et al., 1983
Rhipicephalus oculatus	A	Namibia	Horak et al., 1983
Rhipicephalus follis	A	Swaziland	Gallivan & Surgeoner, 1995
Rhipicephalus masculatus	A	Swaziland	Gallivan & Surgeoner, 1995
Rhipicephalus muehlensi	A N	Swaziland	Gallivan & Surgeoner, 1995
Rhipicephalus gertrudae	-	Free State	Matthee et al., 2013
Argasid ticks			
Ornithodoros porcinus	N	Hoedespruit	Boomker et al., 1991
	N	KNP	Horak et al., 1988
	A	Swaziland	Gallivan & Surgeoner, 1995
Ornithodoros moubata	N	Namibia	Horak et al., 1983

Adapted from Matthee et al., 2013.
A = Adults
N = Nymphs
L = Larvae

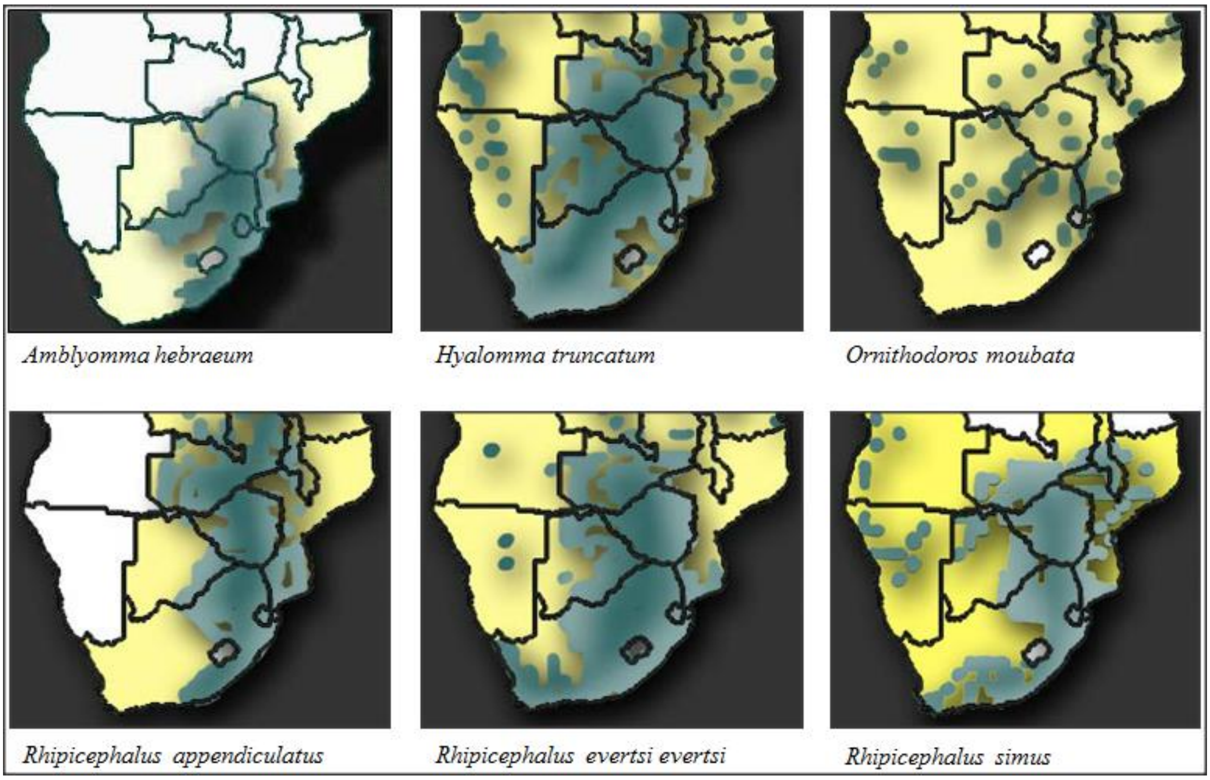

Figure 6: The distribution of tick vectors associated with warthogs in southern Africa (Source: http://www.itg.be/photodatabase/African_ticks_files/index.html).

5 Disease control in South Africa

The Animal Diseases Act No. 35 of 1984 (as amended), Agricultural Product Standards Act No. 119 of 1990 and regulations, and the Meat Safety Act No. 40 of 2000 and regulations, are the legislative acts that govern the management of animal diseases and agricultural products, including meat, in South Africa. The country is also a member of the World Organization for Animal Health (OIE), the intergovernmental organization responsible for improving animal health worldwide that is recognized as a reference organization by the World Trade Organization (WTO). The Department of Agriculture, Forestry and Fisheries (DAFF, 2010), lists the following diseases associated with warthogs as notifiable controlled animal diseases in South Africa (in terms of Animal Diseases Act, Act 35 of 1984); African Swine Fever (ASF), anthrax, Classical Swine Fever (CSF), foot and mouth disease (FMD), trypanosomiasis, rabies, rinderpest, Rift Valley Fever and bovine tuberculosis (bTB). Controlled diseases require that the local/regional state veterinarian is notified of suspected or confirmed cases, who is in turn responsible for taking action according to the control scheme for the specific disease (in terms of section 9 of the Animal Diseases Regulations Act, Act No. R. 2026 of 1986).

Highly infectious diseases such ASF, CSF, FMD and bTB are controlled through demarcated disease control zones in South Africa. The main aim of these control zones is to prevent contact between disease-free and infected populations, and the transmission of infected material from the control zone to disease free zones. Translocations of live cloven hoofed animals and their products from these areas are controlled through stringent surveillance measures, while still allowing the areas to benefit from livestock and game animal production. All live animals and animal product imports and exports, including introduction and translocation of live animals within the country, require permits to certify the animals are free from controlled diseases. Furthermore, active vaccination programs for livestock have been largely successful for controlling heartwater, bTB, anaplasmosis, and to an extent RVF, as well as vaccination of dogs for the rabies virus.

Despite stringent control measures, it is important to remember that South Africa is not immune to possible disease introductions from novel sources (Penrith, 2013), and continued disease surveillance among domestic and wild animals should be a priority for regional and national veterinary and associated authorities. Free-ranging species such as the extra-limital warthogs pose a unique problem as potential disease vectors as they are associated with a number of important animal and zoonotic diseases. This is an important avenue for future research, especially in countries such as South Africa, where the continued expansion of game farming, and combination game/livestock farming, often result in high stocking densities, close proximity of different animal species and frequent animal transportation (Bekker et al., 2012).

In light of the significant shifts in wildlife management and production systems in southern Africa, it has been suggested that surveillance strategies be re-evaluated with the aim to develop more integrated and effective methods for animal and human disease surveillance (Vrbova et al., 2010). Most current disease surveillance methods tend to focus on activities that overlap with livestock and human diseases and might not detect emerging or re-emerging diseases among wildlife (Grogan et al., 2014). Mörner et al. (2002) stated that countries who conduct disease surveys among their wildlife populations are more likely to detect the presence of infectious and zoonotic diseases, and respond more swiftly with counteractive measures, and understanding the ecology of wildlife diseases is pivotal to understanding their epidemiology in animal and zoonotic infections. According to the Training Manual on Wildlife Diseases and Surveillance by the World Organization for Animal Health (OIE, 2010), the surveillance of wildlife diseases consist of four components; the detection of disease among wild populations, the correct identification of disease, the management of information pertaining to the disease and infected populations, and the analysis and communication of the data. The success of each component necessitates that all relevant stakeholders of the agricultural industry, veterinary authorities, and governance bodies work together to develop and implement effective wildlife surveillance strategies (Bekker et al., 2012).

For example, regular serological surveillance surveys among wildlife could evaluate the occurrence and spread of pathogens such as bTB, *Trichinella*, and *E. granulosus* in southern Africa and identify wildlife hosts and specific cohorts of importance. This could aid in the early detection and subsequent management of diseases in wildlife and curb transmission to domestic animal and human populations. It could also prevent the introduction of *Trichinella* to domestic animals and humans, which to date have not been reported in the country. De Lisle et al. (2002) and other authors have referred to the difficulties in obtaining wild animals or animal samples for post-mortem disease inspection. Here the hunting industry provides an ideal situation for robust sampling of wildlife, if hunters and veterinary associations can form partnerships where hunters provide specimens for disease inspection from the animals they hunt. It is however unlikely that the South African government has the financial and professional support to conduct such operations in the long-term.

As mentioned, there is evidence in support of changing distribution ranges of diseases and disease vectors in southern Africa (Hargreaves et al. 2004, Penrith & Vosloo, 2009, De Garine-Wichatitsky et al., 2010, Matthee et al., 2013, Addendum A). The influence of climate change, increased human transportation/translocation of animals and animal products, and anthropogenic modification of natural environments have all been implicated in the emergence and proliferation of infectious diseases on a global scale (Patz et al., 2000, Van Jaarsveld & Chown, 2001). The game ranching industry in particular requires improved control measures and compliance as the industry continues to expand with significant implications on natural and modified ecosystems and translocation/introduction of animals (Bekker et al., 2012). According to the OIE, adequate disease surveillance and education of parties involved in all aspects of animal production, conservation, veterinary care, game hunting and slaughter/processing should be conducted as education is the most effective method for detecting emerging diseases and the factors that govern their epidemiology.

6 Implications for utilization of warthog meat

The production of meat from wild animals has been suggested as a low-input, high production alternative to traditional animal husbandry (Carruthers, 2005, Van Schalkwyk et al., 2010, Kiley-Worthington, 2014). Promoters of game meat consumption maintain that utilizing wild animals contributes towards sustainable wildlife and habitat management, and local food security, while generating an income from a widely available resource (Barnes & De Jager,1996, White & Lowe, 2008, Poshiwa et al., 2013, Chaminuka et al., 2014). Also, the consumption of game meat is an important factor that promotes the social acceptability of hunting (Ljung et al., 2012).

During the six month hunting season, game meat contributes approximately 10% of red meat utilized per annum in South Africa, which was estimated at around 1 249 000 tons during 2011/2012 (DAFF, 2013b). While warthog meat is regularly consumed by rural communities and in informal markets, it is becoming more widely known and utilized in formal markets. Hoffman et al. (2005b) found warthog to be a game meat regularly consumed in South Africa and South African restaurants. Similar to other game animals and game meat, warthogs have a high dressing percentage, low total intramuscular lipid content, high total protein and moisture content and a favorable fatty acid profile (Hoffman & Sales, 2007, Swanepoel et al., 2014, Chapter 5), and suitable organoleptic and technological properties for the use in processed product. Regardless of these findings, the meat from hunted carcasses is still relatively under-utilized by hunters and/or the commercial sector (Hoffman et al., 2005b), possibly due to the lack of information regarding the safety and preparation of the meat.

The Food and Agriculture Organization of the United Nations and the World Health Organization (FAO/WHO, 2014) released a multi-criteria based ranking list of the most important food-borne parasites that pose a risk to humans. The parasites of warthogs that appear on the list in descending order of importance are *E. granulosus, Trichinella* spp., and *Sarcocystis* spp. All of these diseases are transmitted to humans when raw or undercooked meat from infected animals is ingested.

Although warthogs are able to carry and transmit diseases to humans, there is a lack of documented cases of this occurring in southern Africa. There are a number of potential reasons for this. It is very likely that zoonotic infections from warthog-associated parasites are underreported or misdiagnosed, or the role of warthogs as the source of infection is underappreciated in people who regularly consume bushmeat or meat from rural animals. Alternatively, it is also possible that the majority of warthogs are harvested from outside of known zoonotic distribution ranges, such as the KNP, and that potential zoonosis are effectively controlled through current disease management programs and control zones. In South Africa for example, *E. granulosus* appears to be limited to the northern bushveld region of the Limpopo province and KNP (Horak et al., 1988, Boomker et al., 1991, Van Wyk & Boomker, 2011), and *Sarcosystis* spp. associated with warthogs to the KNP (Stolte et al., 1998).

If this is the case then warthog meat has the potential to become part of the formal game meat spectrum if sourced from disease free areas and/or processed according to regulations as set out in the "Meat Inspection Manual: Game" by the Directorate: Veterinary Services of the Department of Agriculture (2007). To encourage the future safe utilization of warthogs in South Africa, it is suggested that hunters and butchers of game meat continue to equip themselves with knowledge on how to visually inspect warthog carcasses destined for human consumption for abnormalities in the organ tissues and the presence of visible parasites and cysts. Additional precautions would include abattoirs that specialize in the commercial production of game meat to regularly have their meat analyzed by accredited laboratories for the presence of infectious agents (Mörner et al., 2002). Furthermore, disease surveillance surveys should continually provide information to farmers, hunters and game meat abattoirs on the prevalence of zoonotic diseases among wildlife populations outside of disease control zones.

7 Conclusion

Free-ranging species such as the extra-limital warthogs pose a unique problem as potential disease vectors, as they are associated with a number of important animal and zoonotic diseases. Future research should investigate the risk of introduced warthog populations in spreading and maintaining diseases, and more specifically the possible routes of disease transmission across their expanding distribution range in South Africa. This is necessary as warthogs will remain a popular species for recreation hunting and meat production purposes, with both trained and untrained persons handling and processing carcasses. Current disease surveillance and control among domestic and wild animals should be re-evaluated to include the risks associated with free-ranging wildlife and expanded distribution ranges of wildlife.

8 References

Ahl, A. S., Nganwa, D., & Wilson, S. (2002). Public health considerations in human consumption of wild game. *Annals of the New York Academy of Science, 969*, 48–50.

Archer, B. N., Thomas, J., Weyer, J., Cengimbo, A., Landoh, D. E., Jacobs, C., … Blumberg, L. (2013). Epidemiologic investigations into outbreaks of Rift Valley Fever in humans, South Africa, 2008-2011. *Emerging Infectious Diseases*, *19*, 2008–2011. doi:10.3201/eid1912.121527

Arnot, L. F., Du Toit, J. T., & Bastos, A. D. S. (2009). Molecular monitoring of African swine fever virus using surveys targeted at adult *Ornithodoros* ticks: A re-evaluation of Mkuze game reserve, South Africa. *The Onderstepoort Journal of Veterinary Research*, *76*, 385–392. doi:10.4102/ojvr.v76i4.22

Arzt, J., Baxt, B., Grubman, M. J., Jackson, T., Juleff, N., Rhyan, J., … Rodriguez, L. L. (2011). The pathogenesis of Foot-and-Mouth Disease II: Viral pathways in swine, small ruminants, and wildlife; myotropism, chronic syndromes, and molecular virus-host interactions. *Transboundary and Emerging Diseases*, *58*, 305-326. doi:10.1111/j.1865-1682.2011.01236.x

Bamford, A. J., Ferrol-Schulte, D., & Wathan, J. (2014). Human and wildlife usage of a protected area buffer zone in an area of high immigration. *Oryx*, *48*, 504–513. doi:10.1017/S0030605313000215

Barnes, J. I., & de Jager, J. V. (1996). Economic and financial incentives for wildlife incentives on private land in Namibia and the implications for policy. *South African Journal of Wildlife Research*, *26*, 1–24.

Bekker, J. L., Hoffman, L. C., & Jooste, P. J. (2012). Wildlife-associated zoonotic diseases in some southern African countries in relation to game meat safety: A review. *The Onderstepoort Journal of Veterinary Research*, *79*, E1–E12. doi:10.4102/ojvr.v79i1.422

Bengis, R. G., & Veary, C. M. (1997). Public health risks associated with the utilisation of wildlife products in certain regions of Africa. *Revue Scientifique et Technique (OIE)*, *16*, 586–593.

Bengis, R. G., & Erasmus, J. M. (1988). Wildlife diseases in South Africa: A review. *Revue Scientifique et Technique, (OIE)*, *7*, 807–821.

Bengis, R. G., Kock, R. A., & Fischer, J. (2002). Infectious animal diseases: the wildlife/livestock interface. *Revue Scientifique et Technique (OIE)*, *21*, 53–65.

Benson, D. E. (1991). Values and management of wildlife and recreation on private land in South Africa. *Wildlife Society Bulletin*, *19*, 497–510.

Bishop, G. C., Durrheim, D. N., Kloeck, P. E., Godlonton, J. D., Bingham, J., Speare, R., & Rabies Advisory Group. (2003). *Rabies: Guide for the medical, veterinary and allied professions*. *In* L. Blumberg, J. Weyer, H. Pienaar, W. Markotter, & Rabies Advisory Group (Eds.) (2nd ed.). Pretoria, South Africa: Government Printer.

Boomker, J., Horak, I. G., Booyse, D. G., & Meyer, S. (1991). Parasites of South African wildlife. VIII. Helminth and arthropod parasites of warthogs, *Phacochoerus aethiopicus*, in the eastern Transvaal. *The Onderstepoort Journal of Veterinary Research*, *58,* 195-202.

Boshoff, C. I., Bastos, A. D. S., Dube, M. M., & Heath, L. (2014). First molecular assessment of the African swine fever virus status of *Ornithodoros* ticks from Swaziland. *Onderstepoort Journal of Veterinary Research*, *81*, 1–5. doi:10.4102/ojvr.v81i1.846

Britch, S. C., Binepal, Y. S., Ruder, M. G., Kariithi, H. M., Linthicum, K. J., Anyamba, A., … Wilson, W. C. (2013). Rift Valley Fever risk map model and seroprevalence in selected wild ungulates and camels from Kenya. *PLoS ONE*, *81*, 1–5. doi:10.1371/journal.pone.0066626

Carruthers, J. (2005). " Wilding the farm or farming the wild "? The evolution of scientific game ranching in South Africa from the 1960s to the present. *Transactions of the Royal Society of South Africa*, *63*, 160–181.

Castley, J. G., Boshoff, A. F., & Kerley, G. I. H. (2001). Compromising South Africa's natural biodiversity - inappropriate herbivore introductions. *South African Journal of Science*, *97*, 344–348.

Chaminuka, P., Udo, H. M. J., Eilers, K. C. H. A. M., & Van der Zijpp, A. (2014). Livelihood roles of cattle and prospects for alternative land uses at the wildlife / livestock interface in South Africa. *Land Use Policy*, *38*, 80–90. doi:10.1016/j.landusepol.2013.10.007

Cheadle, M. A., Spencer, J. A., & Blagburn, B. L. (1999). Seroprevalences of *Neospora caninum* and *Toxoplasma gondii* in nondomestic felids from southern Africa. *Journal of Zoo and Wildlife Medicine : Official Publication of the American Association of Zoo Veterinarians*, *30*, 248–251. doi:10.2307/20095852

Child, B. A, Musengezi, J., Parent, G. D., & Child, G. F. T. (2012). The economics and institutional economics of wildlife on private land in Africa. *Pastoralism: Research, Policy and Practice*, *2*, 18. doi:10.1186/2041-7136-2-18

Cloete, P. C., Taljaard, P. R., & Grové, B. (2007). A comparative economic case study of switching from cattle farming to game ranching in the Northern Cape Province. *South African Journal of Wildlife Research*, *37*, 71–78. doi:10.3957/0379-4369-37.1.71

Costard, S., Wieland, B., de Glanville, W., Jori, F., Rowlands, R., Vosloo, W., … Dixon, L. K. (2009). African swine fever: how can global spread be prevented? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *364*, 2683–2696. doi:10.1098/rstb.2009.0098

Cousins, J. A., Sadler, J. P., & Evans, J. (2010). The challenge of regulating private wildlife ranches for conservation in South Africa. *Ecology and Society, 15,* 28.

Daszak, P., Cunningham, A. A., & Hyatt, A. D. (2000). Emerging infectious diseases of wildlife: threats to biodiversity and human health. *Science*, *287*, 443–449. doi:10.1126/science.287.5452.443

De Garine-Wichatitsky, M., Caron, A., Gomo, C., Foggin, C., Dutlow, K., Pfukenyl, D., … Michel, A. (2010). Bovine Tuberculosis in buffaloes, South Africa. *Emerging Infectious Diseases*, *16*, 884–885. doi:10.1890/02-5266

De Lisle, G. W., Bengis, R. G., Schmitt, S. M., & O'Brien, D. J. (2002). Tuberculosis in free-ranging wildlife : detection, diagnosis and management. *Review of Science and Technology, (OIE)*, *21*, 317–334.

De Vos, V., Bengis, R. G., Kriek, N. P. J., Michel, A., Keet, D. F., Raath, J. P., & Huchzermeyer, H. F. K. A. (2001). The epidemiology of tuberculosis in free-ranging African buffalo (*Syncerus caffer*) in the Kruger National Park, South Africa. *Onderstepoort Journal of Veterinary Research*, *68*, 119–130.

De Waal, D. T. (2000). Anaplasmosis control and diagnosis in South Africa. *Annals of the New York Academy of Sciences*, *916*, 474–483. doi:10.1111/j.1749-6632.2000.tb05327.x

Department of Agriculture, Forestry and Fisheries (DAFF). (2013a). *South African Yearbook 2012/13: Agriculture, Forestry and Fisheries*. In A. Vermeulen (Ed.). Pretoria, South Africa: Department of Agriculture, Forestry and Fisheries. Retrieved from http://www.gcis.gov.za.

Department of Agriculture, Forestry and Fisheries (DAFF). (2013b). *Abstract of Agricultural Statistics 2013*. Compiled by Directorate Statistics and Economic Analysis. Pretoria, South Africa: Department of Agriculture, Forestry and Fisheries. Retrieved from www.nda.agric.za

Department of Agriculture, Forestry and Fisheries (DAFF). (2013c). *Bovine Tuberculosis Scheme Manual*. Pretoria, South Africa: Department of Agriculture, Forestry and Fisheries. Retrieved from http://www.nda.agric.za/vetweb/pamphlets&Information/Policy/TB%20Manual%20%206Dec2013%20interim%20signed.pdf

Department of Agriculture, Forestry and Fisheries (DAFF). (2010). List of controlled and notifiable animal diseases (Act 35 of 1984). Pretoria, South Africa: Department of Agriculture, Forestry and Fisheries. Retrieved from http://ruvasa.co.za/wp-content/uploads/sites/5/2015/07/List-of-controlled-and-notifiable-animal-diseases.pdf

Department of Agriculture, Forestry and Fisheries (DAFF). (2015). Foot-and-mouth disease (media statement). Pretoria, South Africa: Department of Agriculture, Forestry and Fisheries. Retrieved from http://www.redmeatsa.co.za/wp-content/uploads/2015/01/Media_statement_FMD-status-13-Jan-2015.pdf

Department of Environmental Affairs (DEA). (2015). National Environmental Management: Biodiversity Act, 2004 (Act No. 10 of 2004). *Norms and standards for the translocation of indigenous species in South Africa. Volume 595, Government Gazette (38395).* Pages 1–16. Government Printer: Pretoria, South Africa. Retrieved from www.gpwinline.co.za. doi:http://dx.doi.org/9771682584003-32963. Accessed 15 May 2014.

Dhama, K., Chakraborty, S., Kapoor, S., Tiwari, R., Kumar, A., Deb, R., & Rajagunalan, S. (2013). One World, One Health - Veterinary Perspectives. *Advances in Animal and Veterinary Sciences*, *1*, 5–13.

Dobson, A., & Foufopoulos, J. (2001). Emerging infectious pathogens of wildlife. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *356*, 1001–1012. doi:10.1098/rstb.2001.0900

Dubey, J. P., Schares, G., & Ortega-Mora, L. M. (2007). Epidemiology and control of neosporosis and *Neospora caninum*. *Clinical Microbiology Reviews*, *20*, 323–367. doi:10.1128/CMR.00031-06

Dupouy-Camet, J., Lecam, S., Talabani, H., & Ancelle, T. (2009). Trichinellosis acquired in Senegal from warthog ham, March 2009. *Eurosurveillance*, *14*, 1–2.

Dyason, E. (2010). Summary of foot-and-mouth disease outbreaks reported in and around the Kruger National Park, South Africa, between 1970 and 2009. *Journal of the South African Veterinary Association*, *81*, 201–206.

Edwards, S., Fukusho, A., Lefèvre, P. C., Lipowski, A., Pejsak, Z., Roehe, P., & Westergaard, J. (2000). Classical swine fever: The global situation. *Veterinary Microbiology*, *73*, 103–119. doi:10.1016/S0378-1135(00)00138-3

Evans, A., Gakuya, F., Paweska, J. T., Rostal, M., Akoolo, L., Van Vuren, P. J., … Kariuki Njenga, M. (2008). Prevalence of antibodies against Rift Valley fever virus in Kenyan wildlife. *Epidemiology and Infection*, *136*, 1261–1269. doi:10.1017/S0950268807009806.

Everett, H., Crooke, R., Gurrala, R., Dwarke, R., Kim, J., Botha, B., … Drew, T. (2011). Experimental infection of common warthogs (*Phacochoerus africanus*) and bushpigs (*Potamochoerus larvatus*) with Classical Swine Fever Virus I: Susceptibility and transmission. *Transboundary and Emerging Diseases*, *58*, 128–134. doi:10.1111/j.1865-1682.2010.01191.x

Ferroglio, E., Wambwa, E., Castiello, M., Trisciuoglio, A., Prouteau, A., Pradere, E., … De Meneghi, D. (2003). Antibodies to *Neospora caninum* in wild animals from Kenya, East Africa. *Veterinary Parasitology*, *118*, 43–49. doi:10.1016/j.vetpar.2003.09.006

Fitzgerald, S. D., & Kaneene, J. B. (2013). Wildlife reservoirs of bovine tuberculosis worldwide: hosts, pathology, surveillance, and control. *Veterinary Pathology*, *50*, 488–99. doi:10.1177/0300985812467472

Food and Agriculture Organization of the United Nations/World Health Organization (FAO/WHO). (2014). *Multicriteria-based ranking for risk management of food-borne parasites. Microbiological Risk Assessment Series No. 23*. Rome, www.fao.org/3/a-i3649e.pdf\nfiles/540/a-i3649e.pdf.

Gallardo, C., Okoth, E., Pelayo, V., Anchuelo, R., Martín, E., Simón, A., … Bishop, R. P. (2011). African Swine fever viruses with two different genotypes, both of which occur in domestic pigs, are associated with ticks and adult warthogs, respectively, at a single geographical site. *Journal of General Virology*, *92*, 432–444. doi:10.1099/vir.0.025874-0

Gallivan, G. J., & Surgeoner, G. A. (1995). Ixodid ticks and other ectoparasites of wild ungulates in Swaziland: Regional, host and seasonal patterns. *South African Journal of Zoology*, *30*, 169–177.

Gamble, H. R., Bessonov, A. S., Cuperlovic, K., Gajadhar, A. A., Van Knapen, F., Noeckler, K., … Zhu, X. (2000). International commission on trichinellosis: Recommendations on methods for the control of *Trichinella* in domestic and wild animals intended for human consumption. *Veterinary Parasitology*, *93*, 393–408.

Gillingwater, K., Mamabolo, M. V, & Majiwa, P. A. O. (2010). Prevalence of mixed *Trypanosoma congolense* infections in livestock and tsetse in KwaZulu-Natal, South Africa. *Journal of the South African Veterinary Association*, *81*, 219–223. doi:10.4102/jsava.v81i4.151

Gorenflot, A., Moubri, K., Precigout, E., & Carcy, B. (1998). Human babesiosis. *Annals of Tropical Medicine and Parasitology*, *92*, 489–501. doi:10.1126/science.556864

Grange, J. M. (2001). *Mycobacterium bovis* infection in human beings. *Tuberculosis*, *81*, 71–77. doi:10.1054/tube.2000.0263

Gray, J., Zintl, A., Hildebrandt, A., Hunfeld, K. P., & Weiss, L. (2010). Zoonotic babesiosis: Overview of the disease and novel aspects of pathogen identity. *Ticks and Tick-Borne Diseases*, *1*, 3–10. doi:10.1016/j.ttbdis.2009.11.003

Grogan, L. F., Berger, L., Rose, K., Grillo, V., Cashins, S. D., & Skerratt, L. F. (2014). Surveillance for emerging biodiversity diseases of wildlife. *PLoS Pathogens*, *10*, 3–6. doi:10.1371/journal.ppat.1004015

Hargreaves, S. K., Foggin, C. M., Anderson, E. C., Bastos, A. D. S., Thomson, G. R., Ferris, N. P., & Knowles, N. J. (2004). An investigation into the source and spread of foot and mouth disease virus from a wildlife conservancy in Zimbabwe. *Revue Scientifique et Technique (OIE)*, *23*, 783–790.

Hedger, R. S., Condy, J. B., & Golding, S. M. (1972). Infection of some species of African wildlife with Foot-and-mouth disease virus. *Journal of Comparative Pathology*, *82*, 455–461.

Hedger, R. (1972). Foot-and-mouth disease and the African buffalo (*Syncerus caffer*). *Journal of Comparative Pathology*, *82*, 19–28.

Hlokwe, T. M., van Helden, P., & Michel, A. L. (2014). Evidence of increasing intra and inter-species transmission of *Mycobacterium bovis* in South Africa: Are we losing the battle? *Preventive Veterinary Medicine*, *115*, 10–17. doi:10.1016/j.prevetmed.2014.03.011

Hoffman, L. C., & Cawthorn, D.-M. (2012). What is the role and contribution of meat from wildlife in providing high quality protein for consumption? *Animal Frontiers*, *2*, 40–53. doi:10.2527/af.2012-0061

Horak, I. G., Boomker, J., De Vos, V., & Potgieter, F. T. (1988). Parasites of domestic and wild animals in South Africa. XXIII. Helminth and Artropod parasites of warthogs, *Phacochoerus aethiopicus*, in the Eastern Transvaal lowveld. *Onderstepoort Journal of Veterinary Research*, *55*, 145–152.

Horak, I. G., Biggs, H. C., Hanssen, T. S., & Hanssen, R. E. (1983). The prevalence of helminth and arthropod parasites of warthog, *Phacochoerus aethiopicus*, South West Africa/Namibia. *Onderstepoort Journal of Veterinary Research*, *50*, 145-148.

Hove, T., & Dubey, J. P. (1999). Prevalence of *Toxoplasma gondii* antibodies in sera of domestic pigs and some wild game species from Zimbabwe. *The Journal of Parasitology*, *85*, 372–373. doi:10.2307/3285650

Hove, T., & Mukaratirwa, S. (2005). Seroprevalence of *Toxoplasma gondii* in farm-reared ostriches and wild game species from Zimbabwe. *Acta Tropica*, *94*, 49–53. doi:10.1016/j.actatropica.2004.10.010

Hugh-Jones, M. E., & De Vos, V. (2002). Anthrax and wildlife. *Revue Scientifique Et Technique (OIE)*, *21*, 359–383.

Hüttner, M., Siefert, L., Mackenstedt, U., & Romig, T. (2009). A survey of *Echinococcus* species in wild carnivores and livestock in East Africa. *International Journal for Parasitology*, *39*, 1269–1276. doi:10.1016/j.ijpara.2009.02.015

Ito, A., Putra, M. I., Subahar, R., Sato, M. O., Okamoto, M., Sako, Y., … Margono, S. S. (2002). Dogs as alternative intermediate hosts of *Taenia solium* in Papua (Irian Jaya), Indonesia confirmed by highly specific ELISA and immunoblot using native and recombinant antigens and mitochondrial DNA analysis. *Journal of Helminthology*, *76*, 311–314. doi:10.1079/JOH2002128

Jenkins, D. J., & Macpherson, C. N. L. (2003). Transmission ecology of *Echinococcus* in wild-life in Australia and Africa. *Parasitology*, *127,*, S63–S72. doi:10.1017/S0031182003003871

Jensenius, M., Fournier, P., Kelly, P., Myrvang, B., & Raoult, D. (2003). Review African tick bite fever. *The Lancet*, *3*, 557–564. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12954562

Jori, F., & Bastos, A. D. S. (2009). Role of wild suids in the epidemiology of African Swine fever. *EcoHealth, 6,* 296-310. doi:10.1007/s10393-009-0248-7

Jori, F., Brahmbhatt, D., Fosgate, G. T., Thompson, P. N., Budke, C., Ward, M. P., … Gummow, B. (2011). A questionnaire-based evaluation of the veterinary cordon fence separating wildlife and livestock along the boundary of the Kruger National Park, South Africa. *Preventive Veterinary Medicine*, *100*, 210–220. doi:10.1016/j.prevetmed.2011.03.015

Jori, F., Vial, L., Penrith, M. L., Pérez-Sánchez, R., Etter, E., Albina, E., … Roger, F. (2013). Review of the sylvatic cycle of African Swine fever in sub-Saharan Africa and the Indian ocean. *Virus Research*, *173*, 212–227. doi:10.1016/j.virusres.2012.10.005

Kalema-Zikusoka, G., Bengis, R. G., Michel, A. L., & Woodford, M. H. (2005). A preliminary investigation of tuberculosis and other diseases in African buffalo (*Syncerus caffer*) in Queen Elizabeth National Park, Uganda. *The Onderstepoort Journal of Veterinary Research*, *72*, 145–151.

Kiley-Worthington, M. (2014). Ecological agriculture: Integrating low input , high productive farming with wildlife conservation. results from the experimental farm La Combe , Drome France. *Open Journal of Ecology*, *4*, 744–763.

Kruse, H., Kirkemo, A. M., & Handeland, K. (2004). Wildlife as source of zoonotic infections. *Emerging Infectious Diseases*, *10*, 2067–2072. doi:10.3201/eid1012.040707

LaBeaud, A. D., Kazura, J. W., & King, C. H. (2010). Advances in Rift Valley fever research: insights for disease prevention. *Current Opinion in Infectious Diseases*, *23*, 403–408. doi:10.1097/QCO.0b013e32833c3da6

LaBeaud, D. (2011). Towards a safe, effective vaccine for Rift Valley fever virus. *Future Virology*, *5*, 675–678. doi:10.2217/fvl.10.63.

Lembo, T., Hampson, K., Auty, H., Beesley, C. A., Bessell, P., Packer, C., … Cleaveland, S. (2011). Serologic surveillance of anthrax in the Serengeti ecosystem, Tanzania, 1996-2009. *Emerging Infectious Diseases*, *17*, 387–394. doi:10.3201/eid1703.101290

Lindsey, P. A., Havemann, C. P., Lines, R. M., Price, A. E., Retief, T. A., Rhebergen, T., … Romañach, S. S. (2013). Benefits of wildlife-based land uses on private lands in Namibia and limitations affecting their development. *Oryx*, *47*, 41–53. doi:10.1017/S0030605311001049

Ljung, P. E., Riley, S. J., Heberlein, T. A., & Ericsson, G. (2012). Eat prey and love: Game-meat consumption and attitudes toward hunting. *Wildlife Society Bulletin*, *36*, 669–675. doi:10.1002/wsb.208

Luxmoore, R. (1985). Game farming in South Africa as a force in conservation. *Oryx, 19*, 225–231.

Madder M, Horak I, Stoltsz H. (2013). *Ticks: Tick importance and disease transmission*. Retrieved from www.afrivip.org/education/arthropod-vectors/ticks/tick-importance/2013/materials.

Stellenbosch University http://scholar.sun.ac.za

Magwedere, K., Sithole, F., Hoffman, L. C., Hemberger, Y. M., & Dziva, F. (2013). Investigating the contributing factors to postmortem pH changes in springbok, eland, red hartebeest and kudu edible offal. *Journal of the South African Veterinary Association*, *84*, E1–7. doi:10.4102/jsava.v84i1.919

Martin, A., Caro, T., & Borgerhoff Mulder, M. (2012). Bushmeat consumption in western Tanzania: A comparative analysis from the same ecosystem. *Tropical Conservation Science*, *5*, 352–364.

Marucci, G., La Grange, L. J., La Rosa, G., & Pozio, E. (2009). *Trichinella nelsoni* and *Trichinella T8* mixed infection in a lion (*Panthera leo*) of the Kruger National Park (South Africa). *Veterinary Parasitology*, *159*, 225–228. doi:10.1016/j.vetpar.2008.10.041

Matthee, S., Swanepoel, M., Van der Mescht, L., Leslie, A. J., & Hoffman, L. C. (2013). Ectoparasites of a non-indigenous warthog population, *Phacochoerus africanus*, in the Free State Province, South Africa. *South African Journal of Wildlife Research*, *48*, 259–265. doi:10.3377/004.048.0210

Meng, X. J., Lindsay, D. S., & Sriranganathan, N. (2009). Wild boars as sources for infectious diseases in livestock and humans. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *364*, 2697–707. doi:10.1098/rstb.2009.0086.

Michel, A. L., Bengis, R. G., Keet, D. F., Hofmeyr, M., De Klerk, L. M., Cross, P. C., … Godfroid, J. (2006). Wildlife tuberculosis in South African conservation areas: Implications and challenges. *Veterinary Microbiology*, *112*, 91–100. doi:10.1016/j.vetmic.2005.11.035

Miller, R. S., Farnsworth, M. L., & Malmberg, J. L. (2013). Diseases at the livestock-wildlife interface: Status, challenges, and opportunities in the United States. *Preventive Veterinary Medicine*, *110*, 119–132. doi:10.1016/j.prevetmed.2012.11.021

Moennig, V. (2000). Introduction to classical swine fever: virus, disease and control policy. *Veterinary Microbiology*, *73*, 93–102. doi:S0378-1135(00)00137-1 [pii]

Moennig, V., Floegel-Niesmann, G., & Greiser-Wilke, I. (2003). Clinical Signs and epidemiology of classical swine fever: A review of new knowledge. *The Veterinary Journal*, *165*, 11–20. doi:10.1016/S1090-0233(02)00112-0

Molyneux, D., Hallaj, Z., Keusch, G. T., McManus, D. P., Ngowi, H., Cleaveland, S., … Kioy, D. (2011). Zoonoses and marginalised infectious diseases of poverty: where do we stand? *Parasites & Vectors*, *4*, 106. doi:10.1186/1756-3305-4-106

Mörner, T., Obendorf, D. L., Artois, M., & Woodford, M. H. (2002). Surveillance and monitoring of wildlife diseases. *Revue Scientifique et Technique (OIE)*, *21*, 67–76.

Mukaratirwa, S., La Grange, L., & Pfukenyi, D. M. (2013). *Trichinella* infections in animals and humans in sub-Saharan Africa: A review. *Acta Tropica*, *125*, 82–9. doi:10.1016/j.actatropica.2012.09.005.

Mutshembele, A. M., Cabezas-Cruz, A., Mtshali, M. S., Thekisoe, O. M. M., Galindo, R. C., & de la Fuente, J. (2014). Epidemiology and evolution of the genetic variability of *Anaplasma* *marginale* in South Africa. *Ticks and Tick-Borne Diseases*, *5*, 624–631. doi:10.1016/j.ttbdis.2014.04.011

National Institute for Communicable Diseases (NICD). (2014). *Anthrax. Communicable Diseases Communiqué, 13*, 1–3. Retrieved from www.nicd.ac.za/assets/files/NICD-NHLS%20AnthraX.pdf.

Nyafu, K. 2009. *Warthog as an introduced species in the Eastern Cape*. MSc Thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

Oberem P, & Oberem O. (2011). *A Guide to Animal Diseases in South Africa: Game*. Pretoria: Briza publications.

Ocaido, M., Siefert, L., & Baranga, J. (1996). Disease surveillance in mixed livestock and game areas around Lake Mburo National Park in Uganda. *South African Journal of Wildlife Research*, *26*, 133–135.

Otero-Abad, B., & Torgerson, P. R. (2013). A systematic review of the epidemiology of *Echinococcosis* in domestic and wild animals. *PLoS Neglected Tropical Diseases*, *7*, e2249. doi:10.1371/journal.pntd.0002249

Patz, J. A., Graczyk, T. K., Geller, N., & Vittor, A. (2000). Effects of environmental change on emerging parasitic diseases. *International Journal for Parasitology*, *30*, 1395–1405. doi:10.1016/S0020-7519(00)00141-7

Paweska, J. T. (2014). Rift Valley fever. In Ö. Ergönul, F. Can, M. Akova, L. Madoff. (Eds.), *Emerging infectious diseases: Clinical case studies* (pp 73–93). London, England: Academic Press.

Penrith, M.-L. (2009). African swine fever. *The Onderstepoort Journal of Veterinary Research*, *76*, 91–95.

Penrith, M. L., Thomson, G. R., Bastos, A. D. S., Phiri, O. C., Lubisi, B. A., Du Plessis, E. C., … Esterhuysen, J. (2004). An investigation into natural resistance to African swine fever in domestic pigs from an endemic area in southern Africa. *Revue Scientifique et Technique (OIE)*, *23*, 965–977.

Penrith, M. L., Vosloo, W., & Mather, C. (2011). Classical Swine fever (Hog cholera): Review of aspects relevant to control. *Transboundary and Emerging Diseases*, *58*, 187–196. doi:10.1111/j.1865-1682.2011.01205.x

Penrith, M. L. (2013). History of "swine fever" in Southern Africa. *Journal of the South African Veterinary Association*, *84*, 1–6. doi:10.4102/jsava.v84i1.1106

Penzhorn, B. L. (1971). A summary of the reintroduction of ungulates into South African National Parks (to 31 December 1970). *Koedoe*, *14*, 145–159.

Pepin, M., Bouloy, M., Bird, B. H., Kemp, A., & Paweska, J. (2010). Rift Valley fever virus (Bunyaviridae: Phlebovirus): An update on pathogenesis, molecular epidemiology, vectors, diagnostics and prevention. *Veterinary Research*, *41*, 61–101. doi:10.1051/vetres/2010033

Peter, T., Anderson, E., Burridge, M., & Mahan, S. (1997). Heartwater carrier status in wild African ruminants. *Épidémiologie et Santé Animale*, 31–32.

Peter, T. F., Burridge, M. J., & Mahan, S. M. (2002). *Ehrlichia ruminantium* infection (heartwater) in wild animals. *Trends in Parasitology*, *18*, 214–218. doi:10.1016/S1471-4922(02)02251-1

Pienaar, N. J., & Thompson, P. N. (2013). Temporal and spatial history of Rift Valley fever in South Africa : 1950 to 2011. *Onderstepoort Journal of Veterinary Research*, *80*, 1–13. doi:10.4102/ojvr.v80i1.384

Poshiwa, X., Groeneveld, R. A., Heitkönig, I. M. A., & Prins, H. H. T. (2013). Reducing rural households ' annual income fluctuations due to rainfall variation through diversification of wildlife use : portfolio theory in a case study of south eastern Zimbabwe . *Tropical Conservation Science*, *6*, 201–220.

Pozio, E., Kapel, C. M., Gajadhar, A. A., Boireau, P., Dupouy-Camet, J., & Gamble, H. R. (2006). *Trichinella* in pork: current knowledge on the suitability of freezing as a public health measure. Euro Surveillance, *11,* Article 1. www.eurosurveillance.org/ViewArticle.aspx?ArticleId=3079.

Pozio, E. (2007). World distribution of *Trichinella* spp. infections in animals and humans. *Veterinary Parasitology*, *149*, 3–21. doi:10.1016/j.vetpar.2007.07.002

Prempeh, H., Smith, R., & Müller, B. (2001). Foot and mouth disease: the human consequences. The health consequences are slight, the economic ones huge. *BMJ: British Medical Journal*, *322*, 565–566. doi:10.1136/bmj.322.7286.565

Professional Hunters Association of South Africa (PHASA). (2014). *Revenue from hunting tourists breaks R1 billion mark.* Retrieved from www.phasa.co.za/what-is-in-the-news/phasa-press-release/item/570-revenue-from-hunting-tourists-breaks-r1-billion-mark.html.

Rautenbach, I. L. (1982). Mammals of the Transvaal. *Ecoplan Monograph No.1*. Pretoria, South Africa: Ecoplan.

Renwick, A., White, P. C. L., & Bengis, R. G. (2007). Bovine tuberculosis in southern African wildlife: a multi-species host-pathogen system. *Epidemiology and Infection*, *135*, 529–540. doi:10.1017/S0950268806007205

Rhyan, J. C., & Spraker, T. R. (2010). Emergence of diseases from wildlife reservoirs. *Veterinary Pathology*, *47*, 34–39. doi:10.1177/0300985809354466

Riemann, G. P., Burridge, M. J., Behymer, D. E., & Franti, C. E. (1975). *Toxoplasma gondii* antibodies in free-living African mammals. *Journal of Wildlife Diseases*, *11*, 529–533.

Sciutto, E., Fragoso, G., Fleury, A., Laclette, J. P., Sotelo, J., Aluja, A., … Larralde, C. (2000). *Taenia solium* disease in humans and pigs: An ancient parasitosis disease rooted in developing countries and emerging as a major health problem of global dimensions. *Microbes and Infection*, *2*, 1875–1890. doi:10.1016/S1286-4579(00)01336-8

Sellers, R., & Gloster, J. (2008). Foot-and-mouth disease: A review of intranasal infection of cattle, sheep and pigs. *Veterinary Journal*, *177*, 159–168. doi:10.1016/j.tvjl.2007.03.009

Siembieda, J. L., Kock, R. A, McCracken, T. A., & Newman, S. H. (2011). The role of wildlife in transboundary animal diseases. *Animal Health Research Reviews / Conference of Research Workers in Animal Diseases*, *12*, 95–111. doi:10.1017/S1466252311000041

Spear, D., & Chown, S. L. (2009). Non-indigenous ungulates as a threat to biodiversity. *Journal of Zoology*, *279*, 1–17. doi:10.1111/j.1469-7998.2009.00604.x

Skead, J., Boshoff, A., & Kerley, G. I. H. (2007). Historical incidence of the larger land mammals in the broader Eastern Cape. Port Elizabeth, South Africa: Centre for Conservation Ecology, Nelson Mandela Metropolitan University.

Skinner, J. D., & Chimimba, C. T. (2005). *The mammals of the southern African sub-region*. Cape Town, South Africa: Cambridge University Press

Stewart, C. G., Keffen, R. H., McCrindle, C., Duncan, A. N., & De Waal, D. T. (1991). *Baubesia trautmanni* infection in a warthog (*Phacochoerus aethiopicus*). *Journal of the South African Veterinary Association*, *66*, 98. Retrieved from <Go to ISI>://CABI:19960803075

Stolte, M., Odening, K., Quandt, S., Bengis, R. G., & Bockhardt, I. (1998). *Sarcocystis dubeyella n.* sp. and *Sarcocystis phacochoeri n*. sp. (Protozoa: *Sarcocystidae*) from the Warthog (*Phacochoerus aethiopicus*) in South Africa. *Journal of Eukaryotic Microbiology*, *45*, 101–104.

Tappe, D., & Büttner, D. W. (2009). Diagnosis of human visceral pentastomiasis. *PLoS Neglected Tropical Diseases*, *3*, e320. doi:10.1371/journal.pntd.0000320

Taylor, L. H., Latham, S. M., & Woolhouse, M. E. (2001). Risk factors for human disease emergence. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *356*, 983–989. doi:10.1098/rstb.2001.0888

Thomson, G. R. (1985). The epidemiology of African swine fever: the role of free-living hosts in Africa. *Onderstepoort Journal of Veterinary Research, 52*, 201–209.

Thomson, G. R., Vosloo, W., & Bastos, A. D. S. (2003). Foot and mouth disease in wildlife. *Virus Research*, *91*, 145–161. doi:10.1016/S0168-1702(02)00263-0

Van der Lugt, J. J., Markus, M. B., Kitching, J. P., & Daly, T. J. (1994). Necrotic encephalitis as a manifestation of acute sarcocystosis in cattle. *Journal of the South African Veterinary Association*, *65*, 119–121.

Van der Merwe, P., & Saayman, M. (2003). Determining the economic value of game farm tourism. *Koedoe*, *46*, 103–112. doi:10.4102/koedoe.v46i2.59

Van Jaarsveld, A. S., & Chown, S. L. (2001). Climate change and its impacts in South Africa. *Trends in Ecology & Evolution*, *16*, 13–14. doi:10.1016/S0169-5347(00)02037-1

Van Schalkwyk, D. L., McMillin, K. W., Witthuhn, R. C., & Hoffman, L. C. (2010). The contribution of wildlife to sustainable natural resource utilization in Namibia: A review. *Sustainability*, *2*, 3479–3499. doi:10.3390/su2113479

Van Wyk, I. C., & Boomker, J. (2011). Parasites of South African wildlife. XVIV. The prevalence of helminths in some common antelopes, warthogs and a bushpig in the Limpopo province, South Africa. *Onderstepoort Journal of Veterinary Research*, *78*, 1–11. doi:10.4102/ojvr.v78i1.308

Vrbova, L., Stephen, C., Kasman, N., Boehnke, R., Doyle-Waters, M., Chablitt-Clark, A., … Patrick, D. M. (2010). Systematic review of surveillance systems for emerging zoonoses. *Transboundary and Emerging Diseases*, *57*, 154–161. doi:10.1111/j.1865-1682.2010.01100.x

Wahlers, K., Menezes, C. N., Wong, M. L., Zeyhle, E., Ahmed, M. E., Ocaido, M., … Grobusch, M. P. (2012). Cystic echinococcosis in sub-Saharan Africa. *The Lancet Infectious Diseases*, *12*, 871–880. doi:10.1016/S1473-3099(12)70155-X

Wahlers, K., Menezes, C. N., Romig, T., Kern, P., & Grobusch, M. P. (2013). *Cystic echinococcosis* in South Africa: The worst yet to come? *Acta Tropica*, *128*, 1–6. doi:10.1016/j.actatropica.2013.06.002

Walker, J. B., Keirans, J. E., & Horak, I. G. (2000). *The Genus Rhipicephalus (Acari, Ixodidae): A guide to the brown ticks of the world*. Cambridge, England: Cambridge University Press.

Weyher, A. H., Phillips-Conroy, J. E., Fischer, K., Weil, G. J., Chansa, W., & Fischer, P. U. (2010). Molecular identification of *Schistosoma mattheei* from feces of Kinda (*Papio cynocephalus kindae*) and grayfoot baboons (*Papio ursinus griseipes*) in Zambia. *The Journal of Parasitology*, *96*, 184–190. doi:10.1645/GE-2186.1

White, P. C. L., & Lowe, P. (2008). Wild mammals and the human food chain. *Mammal Review*, *38*, 117–122. doi:10.1111/j.1365-2907.2008.00121.x

Williams, J. H., Espie, I., van Wilpe, E., & Matthee, A. (2002). Neosporosis in a white rhinoceros (*Ceratotherium simum*) calf. *Journal of the South African Veterinary Association*, *73*, 38–43. doi:10.4102/jsava.v73i1.547

World Organisation for Animal Health and World Health Organization (WHO/OIE). (2002). *WHO/OIE manual on Echinococcosis in humans and animals: A public health problem of global concern*. In M. A. Eckert, F. X. Gemmell, Z. Meslin, & S. Pawlowski (Eds.). Paris, France: WHO Press:

World Health Organization (WHO). (2010). *Working to overcome the global impact of neglected tropical diseases: first WHO report on neglected tropical diseases*. Paris, France:WHO Press. Retrieved from http://apps.who.int/iris/handle/10665/44440.

World Health Organization (WHO). (2012). *Research priorities for zoonoses and marginalized infections (Technical report series no. 971)*. Geneva, Switzerland: WHO Press. Retrieved from http://appswho.int/iris/bitstream/10665/75350/1/WHO_TRS_971_eng.pdf

World Health Organization (WHO). (2013). *Rabies country profile: South Africa*. Retrieved from http://www.who.int/rabies/epidemiology/Rabies_CP_SouthAfrica_09_2013.pdf.

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Chapter 4

Farmers' Perceptions of the Extra-limital Common Warthog in the Northern Cape and Free State provinces, South Africa*

Abstract

The common warthog (*Phacochoerus africanus*) has been extra-limitally introduced onto various farms and reserves in parts of the Northern Cape and Free State provinces of South Africa. Warthogs are considered as a game animal for wildlife tourism and hunting but are a known agricultural pest in their natural range. We investigated the perceptions, attitudes, and actions of farmers and landowners toward the common warthog on their farms. We identified participants using the Snowball technique and interviewed them during semistructured personal interviews, conducted from June to October 2012, using a standardized questionnaire. Most farmers and landowners were of the opinion that warthogs were introduced to the area and considered warthog populations to be increasing. Warthogs were held responsible for causing damage to aspects of the natural and agricultural environment, and respondents were increasingly negative toward warthogs as the levels of perceived damages increased. There were, however, also a number of respondents who regarded and utilized the species as a game animal. The majority of respondents hunted warthogs and utilized their meat for consumption; therefore, the study proposes that scientifically based hunting efforts for meat production be implemented to control population numbers and mitigate negative impacts experienced.

Keywords: extra-limital, farmers, hunting, management, *Phacochoerus africanus,* utilization, warthog.

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1 Introduction

Large, terrestrial mammals have typically been introduced outside their range for game farming, sport hunting, meat provision purposes, aesthetics, or conservation (Clout & Russel, 2007, Chown, Spear, Lee, & Shaw, 2009). Ungulate species are among the wildlife most often introduced for these purposes (Spear & Chown, 2009). However, intentionally introduced ungulate species can become naturalized and able to disperse within the surrounding area (Fraser, Cone, & Whitford, 2000, Forsyth & Duncan, 2001). Nonnative wildlife may present a threat to natural and modified habitats and incur environmental and economic costs that lead to increased human–wildlife conflict situations (Pimentel et al., 2001, Lowney, Schoenfeld, Haglan, & Witmer, 2005). These species may also provide benefits to human communities, and a conflict of interest therefore often exists regarding how they are perceived and managed. Feral pigs (*Sus scrofa*), for example, have been introduced onto every continent except Antarctica and are heavily persecuted for damage reprisal, but are also considered a popular game animal for sport hunting and meat production, the main reason they were originally introduced (Bengsen, Gentle, Mitchell, Pearson, & Saunders, 2014).

Both exotic and native wildlife species that are valued as game animals are regularly introduced and/or translocated in South Africa for the game farming industry. Game farming is defined as a production system where wild animals are managed extensively or intensively on private or communal land, exclusively or in conjunction with other agricultural practices, including livestock rearing (Cousins, Sadler, & Evans, 2010). The industry relies on the utilization of wildlife through eco-tourism, recreational hunting, live game sales and meat production for personal or commercial gain (Van der Merwe & Saayman, 2004, Bothma & Du Toit, 2010). The establishment and success of the industry is attributed to the change in wildlife protection policies and private land-ownership during the 1960s and 1970s, which encouraged wildlife protection and utilization on state-owned and private reserves (Luxmoore, 1985, Benson, 1991). Thereby South African law permits landowners full ownership of all the animals that are contained within their property through adequate fencing, making both livestock and wildlife a valuable and tradable commodity.

Species introductions are driven by the demand of tourists and hunters for certain species and a great diversity of species, which is associated with increased economic activity (Barnes & De Jager, 1996, Castley, Boshoff, & Kerley, 2001, Higginbottom & King, 2006). These introductions contribute to the homogenization of South African ungulate species compositions, and escapees (unintentional introductions) often form established naturalized populations (Clout & Russel, 2007, Spear & Chown, 2009). The practice appears to have been facilitated by the country's natural species richness, and the lack of a national framework to govern the game farming industry (Spear & Chown, 2009, Cousins et al. 2010). This has recently been recognized by the Department of Environmental Affairs, which is in the process of developing a national framework for the norms and standards of translocation of indigenous Species (Department of Environmental Affairs [DEA] 2015).

The common warthog (*Phacochoerus africanus*) has been extra-limitally introduced to various game farms and reserves in South Africa since the 1970s (Penzhorn, 1971). The first introductions were conducted by conservation authorities onto provincial reserves in the Eastern Cape, Northern Cape, and the Free State provinces and considered a 'reintroduction' of a warthog species believed to have gone locally extinct (Cape warthog [*P. aethiopicus*]). Introductions onto game farms and game-reserves followed because the species proved to be popular among tourists and hunters. The common warthog is a charismatic species that contributes to tourist satisfaction when viewing wildlife on game farms and reserves (Maciejewski & Kerley, 2014), and it is regularly hunted for recreational purposes. The International Union for Conservation of Nature lists *P. africanus* as a species of 'Least Concern' in South Africa and on the African continent.

Unlike other ungulate species, warthogs are not contained within the borders of a property by standard wire or wire-mesh fencing, and can be considered a 'free-roaming' species in South Africa. Following their introduction into the Eastern Cape in the 1980s, they have become to be regarded as an invasive because of the impacts they exert on the natural and agricultural environment (Nyafu, 2009). A preliminary investigation by our research team (M. Swanepoel et al.) in 2010 found that introduced warthog populations in the Northern Cape and Free State provinces have escaped from their original introduction points and started to reproduce and disperse over large distances to form established, naturalized populations in the new habitat. Warthogs are recognized as agricultural pests in their natural range; they are responsible for financial losses through crop-raiding or by damaging infrastructure (Mason, 1982, Somers, 1992, Vercammen & Mason, 1993). Both the Northern Cape and Free State provinces are important agricultural producers, utilizing the majority of available land for farming purposes. In addition, data collected by this research team indicate that warthogs have become more widespread across the country, with introduced populations expanding their range (M. Swanepoel, unpublished data).

Agricultural producers are regularly in conflict with wildlife that they perceive to threaten their livelihoods (Madden, 2004), and may respond by protecting crops or vulnerable livestock through killing and trapping problem species or transforming habitat to discourage them (Treves, Wallace, Naughton-Treves, & Morales, 2006). However, because farmers recognize that wildlife has a social and economic value, they may simultaneously promote wildlife populations on their farm while trying to mitigate the damages caused (Conover, 1998). The introduced common warthog is therefore part of a unique paradigm where a wildlife species can be considered, and subsequently managed, as either a damage-causing or valuable wildlife species. This conflicting approach to management may result in unethical and unsustainable control practices with undesirable outcomes for both farmers and warthogs. However, farmers' response to introduced warthogs remains unknown. The main objective of this study was to collect baseline information on the interaction between farmers and warthogs in the introduced region. It was proposed that farmers' attitude toward warthogs would be influenced by their perception of introduced warthogs and the impacts associated with warthog presence, and that their behavior toward warthogs would be a reflection of their attitudes and perceptions. The study aimed to gather demographic information on the farmers and farms in the region, investigate whether warthogs have any impacts on the natural and agricultural environment from farmers' perspective, and investigate how farmers perceive and behave toward warthogs.

2 Study area

The study area focused on the region surrounding the city of Kimberley (28°44′31″S, 24°46′19″E) in the Northern Cape province of South Africa, on the border of the Free State Province. The area consisted primarily of Kimberley Thornveld and Western Free State Clay Grassland type vegetation. The grassy, dwarf shrubland of the Kimberley Thornveld region was based largely on rocky, sandy soils, giving rise to mainly hemicryptophytes and chameaphytes (Rutherford & Westfall, 1994). The grass-and-shrub layer was well-developed or may be dominated by thorny shrubs, revealing large patches of uncovered soil. Both the Northern Cape and Free State provinces were important agricultural producers, utilizing the majority of available land for farming purposes. The Northern Cape covered an area of 363,389 km^2 of which 81% was utilized for agricultural purposes. The major agricultural activity was stock farming, including cattle (*Bos taurus*), sheep (*Ovis aries*), and goat (*Capra hircus*). Crop farming only comprised 2% of the total land use because the area is arid. The Free State province covered 129,825 km^2, with agriculture accounting for 90% of the land use, of which approximately 57% was used for livestock farming and 33% for crop production (Department of Agriculture, Forestry and Fisheries [DAFF] 2013). Game farming had also become a major form of agricultural land use, with game farms covering 48,520 km^2 (13.4% of total area) of the Northern Cape and 1,477 km^2 (1.14% of total area) of the Free State provinces.

3 Methods

It is important to note that at the time we conducted the interviews, it was not required by the authors' affiliated institution to obtain ethical clearance for a study that involved interviewing consenting adults; thus, no name of Institutional Review Board or Ethics Committee or approval number or statement is available. In 2010, we conducted a pilot study using the first draft of the questionnaire, before the final draft was drawn up for purpose of this study. We also conducted the pilot study as a method to improve the reliability and validity of the survey. We conducted the survey for the present study from June to

October 2012. We identified farmers and landowners using the Snowball sampling technique (Goodman 1961), where we asked each interviewed farmer to provide the contact details of another farmer who would likely participate in the study. We chose this method for its simplicity and efficiency, considering the time and resource constraints presented to the interviewer in terms of distances travelled and availability of interviewees. The authors knew the first interviewee. We first contacted interviewees and asked if they would be willing to participate in the study, and assured them of full anonymity; after interviewees gave oral consent, then we scheduled a personal interview between the interviewer and the interviewee. Participants documented proof of oral consent, which allowed the interviewer to document their personal details and the details of the scheduled interview. We did not include these details in the data set used for analyses, and we assigned every interviewee a number to allow for anonymous analyses. The personal information of interviewees was only known by the main author, who was responsible for directly interviewing all participants. The main author interviewed 59 total farmers–landowners. The main author did not predetermine the duration of an interview, and interviews ranged between 30 minutes and 2 hours, depending on the amount of interest exhibited by the respondent. We treated all data as confidential.

We used a standardized questionnaire for data collection, and made parts of the questionnaire available as Supporting Material. The questionnaire consisted mainly of close-ended questions, allowing the investigation of general responses and trends within the sample population. The format of the questions was a combination of single answer, contingency, and matrix questions, depending on the type of information required. Some of the questions were followed up with an open-ended question, in case the respondent wanted to explain his or her answer. We structured Section A of the questionnaire to collect demographic information on the respondent: age, gender, occupational role on farm, involvement on farm, and length of tenure; we structured section B to collect information on farm specifics: location of farm, farm size, type of natural vegetation, the primary type of agriculture practiced, the composition and number of livestock and/or game animals kept, the crop types grown and size of fields, type of boundary and paddock fencing used, and the use of electric fencing. Information on the presence of livestock and game-animal predators was also gathered at the end of this section: what predators were present on the farm and whether they were subjected to some form of management. We structured Section C to collect information on the presence of warthogs on the farm; and Section D allowed for open questions (from the interviewer) and further questions and comments (from the interviewee). We present the location of the farms in Fig. 1.

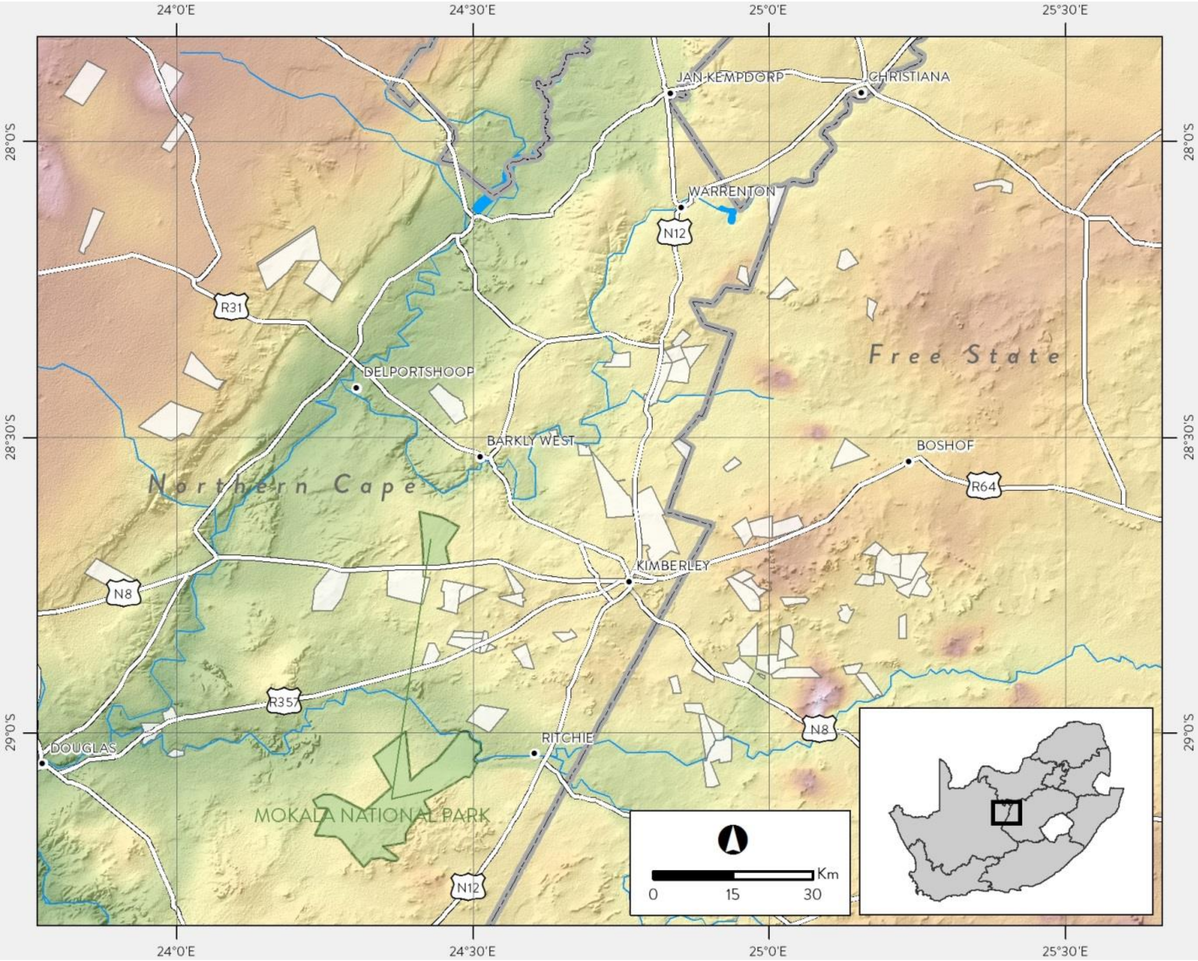

Figure 12. Distribution of the farms in our study area in South Africa, where we surveyed farmers and landowners during June to October 2012 to investigate their perceptions, attitudes, and actions toward the common warthog on their farms.

3.1 Statistical Analysis

We took a quantitative approach in order to measure and statistically analyze perceptions among respondents, rather than a qualitative approach (Babbie & Mouton, 2001). We conducted all tests using STATISTICA (StatSoft, Inc. 2013, version 12; Tulsa, Oklahoma, USA), and we used a 5% level of significance as a guideline for explaining significant differences. We assessed correlations between ordinal variables using Spearman correlation. We used mixed-model analysis of variance to compare categorical variables where >1 option on the questionnaire could be selected with continuous values (e.g., age). We used cross-tabulation with the Chi-square test to compare categorical variables.

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4 Results

All the farmers (*n* = 59) contacted for interviews were willing to participate, and thus the study had a return rate of 100%. The average age of interviewees was 50 years and most (95%) were male (Table 1). Average tenure length was 19 years, with a minimum of 1.5 years and a maximum of 85 years, while the majority (59%) owned the land they farmed and were involved full-time with the farm (63%). The size of properties ranged from 76.6 ha to 12,000 ha, with an average farm size of 2,713.0 ha (SD = ± 2,750.46 ha). Because of the small sample size of primary crop farmers (*n* = 3), they were excluded from the primary land-use analysis. The primary land use (the main focus of the farm) practiced by farmers was livestock farming (63%), followed by game farming (32%) and crop farming (5%). The majority (70%) of primary livestock farmers also had game animals, while half (50%) of primary game farmers also had livestock. Although only 5% of farms were primarily crop farms, 27% of livestock and game farmers also grew crops to varying degrees. The most common crops planted, in declining order, were corn (maize; *Zea mays*), lucerne (*Medicago sativa*), and wheat (*Triticum* spp.).

Table 1: Demographics of farmers interviewed in the Northern Cape and Free State provinces of South Africa between June and October 2012 to investigate their perceptions, attitudes, and actions toward the common warthog on their farms.

Variable	No. of farmers	(%)
Age class (yr)		
20–40	16	27
40–60	29	49
>60	14	24
Length of tenure (yr)		
<10	18	31
10–19	19	32
>20	22	37
Relation to farm		
Land-owner and farmer	35	59
Farmer on leased land	10	17
Manager	11	19
Land-owner	3	5
Involvement		
Full time	37	63
Part time	22	37

The predominant vegetation type on farms (according to farmers) was sweet veld (63%; vegetation type associated with low annual rainfall and high temp), and the remaining (27%) was mixed sweet veld (vegetation consisting of sweet veld and shrub-like vegetation, Acocks, 1988). A combination of fence types were used on farms (Table 2). The prevalent reason for the use of electrical fences was to keep predators out (55% of farmers), while 28% used the fences to keep predators out and game animals inside, and 17% used electrical fences only to keep game inside.

Table 2: Types of boundary and paddock fences used by farmers (n = 59) interviewed in the Northern Cape and Free State provinces of South Africa between June and October 2012 to investigate their perceptions, attitudes, and actions toward the common warthog on their farms.

Type of fence	Boundary fences (%)	Paddock fences (%)
Conventional stock fences	41	65
Game fences	31	17
Part livestock, part game fences	29	14
Electrical fences	15	15

The predators that presented a threat to livestock according to farmers included black-backed jackals (*Canis mesomelas*), caracals (*Caracal caracal*), and leopards (*Panthera pardus*); all farmers interviewed stated they had observed jackals on their property, whereas caracals were observed by 93% of farmers, and leopards were observed by 7% of farmers. Brown hyenas (*Hyaena brunnea*) had been observed by 14% of farmers, and one farmer hunted them for livestock loss reprisal. It should be noted that the brown hyena is listed as 'Near Threatened' by the International Union for Conservation of Nature, and that this hunting is the farmer's own initiative. Some form of predator management was employed by 81% of livestock and 89% of game farmers, which consisted of hunting and the use of traps. Livestock guard dogs were used by 15% of livestock farmers.

Warthogs were present on all farms in the study area (n = 85). The majority (90%) of farmers claimed that warthogs never occurred historically in the area according to their knowledge. Of these respondents, 77% observed warthogs for the first time on their properties between 2000 and 2009, and 21% prior to 2000. None of the farmers that indicated warthogs have always been present in the region had a tenure length exceeding 16 years. Forty-one per cent of farmers guessed that between 10 and 30 warthogs were present at any given time on their farm, with 78% indicating that warthog numbers were increasing. Farmers with larger farms believed they had larger warthog populations compared with farmers with smaller farms ($r = 0.46$, $P < 0.01$). The main view held by farmers (78%) regarding warthog origin was that they were deliberately introduced onto game farms in the region, and escapees dispersed to establish free-roaming populations. Fifty-eight per cent of these farmers could identify the farm where warthogs were introduced, and one farmer knew that warthogs were introduced onto his land prior to his ownership. The alternative view (22%) was that warthogs were expanding their natural range by migrating southward from northern-based meta-populations.

Farmers identified 6 general impacts on the natural and agricultural environments (Table 3). Damage to fences (Fig. 2) was rated the highest, with a mean value of 5.8; and no difference was found between how farmers rated the damage to fences and the type of fences on the farm ($F_{2, 56} = 0.53$, $P = 0.59$), as well as the use of electrified fences ($F_{1, 58} = 0.12$, $P = 0.73$). The overall attitude of farmers was negative ($\bar{x}$ value = 3.9) toward warthogs regarding their impact on the natural environment, as well as the agricultural environment ($\bar{x}$ value = 3.1). However, 14% of respondents hypothesized that some impacts on the natural environment might be positive, such as soil aeration (caused by warthogs uprooting grasses) or by warthogs potentially being prey for predators. Livestock farmers were more negative than game farmers concerning the impacts warthogs have on the agricultural environment ($F_{1, 53} = 7.87$, $P = 0.01$), but not the natural environment ($F_{1, 53} = 2.85$, $P = 0.10$). Overall, farmers were increasingly negative as the level of perceived damage caused by warthogs to veld–plants ($r = -0.45$, $P < 0.01$), soil systems ($r = -0.43$, $P < 0.01$), carrying capacity ($r = -0.48$, $P < 0.01$), fences ($r = -0.54$, $P < 0.01$), and crops–fields ($r = -0.59$, $P < 0.01$) increased. Additional impacts experienced that were not captured in the questionnaire included 1) warthog burrows compromise soil structure and stability; 2) warthogs damage young trees and tree bark, causing trees to die off; 3) warthogs consume feed–mineral lick reserved for livestock or game animals; 4) warthogs incur time, labor, and equipment costs by damaging infrastructure; 5) warthogs physically harm or kill small livestock; and 6) warthogs cause vehicle accidents.

Table 3: General aspects of the natural and agricultural environment on which warthogs have an impact, based on farmers' responses to a survey done between June and October 2012 in the Northern Cape and Free State provinces of South Africa.

Environment	Aspect	Definition
Natural	Veld–plants	Natural vegetation of the area
	Soil	Immediate ground surface
	Carrying capacity	Ability of the area to sustain the number of inhabiting animals
Agricultural	Fences	All fence types including electrified fences
	Water structures	Man-made water provision structures
	Crops–fields	Areas with cultivated plants or produce

Figure 13: Example of damage done by warthogs at a boundary fence on a farm in the Northern Cape province of South Africa (photo by M. Swanepoel).

The majority of farmers (90%) hunted warthogs by 1) active hunting (34%), 2) opportunistic hunting (80%), or 3) hunting by other parties, where outside individuals hunt warthogs on the farm (64%). Livestock farmers who allowed other hunters to hunt warthogs on their farm (62%) made the distinction between "family or friends that want to hunt" as opposed to "hunters who pay to hunt," because they were generally not willing to accommodate the latter. Game farmers allowed "family or friends that want to hunt" as well as "hunters who pay to hunt" on their farms (78%). Traps were used to catch warthogs by 9% of farmers, all of whom were livestock farmers. Farmers who employed opportunistic hunting were increasingly negative toward warthogs ($\bar{x}$ value = 2.6), as were farmers who made use of traps ($\bar{x}$ value = 1.0). Only 2 livestock farmers hunted warthogs with their domestic dogs. Nonlethal management was practiced by 7% of farmers. This included improving the strength of boundary fences by adding extra wires or extending the wire structure beneath the soil surface, or by creating permanent passageways in fences for warthogs to discourage them from creating new holes.

Culled warthogs were utilized by farmers in a wide variety of ways (Fig. 3). Almost half (45%) utilized the meat commercially, meaning they either sold meat to local butcheries or sold meat as part of the hunting package. Twenty-nine percent of respondents allowed warthogs of trophy size to be hunted on their farms for remuneration, but indicated it was a complicated endeavor because warthogs were free-roaming and they could not guarantee that trophy-sized warthogs were present on their farm at any given time. The tushes (the correct term for 'tusks' in this family) are sometimes kept as decorative or novelty items, but the majority (47%) of farmers do not utilize the tushes in any way, as is the case with the animals' hide (91%). One farmer presented a suitcase made from warthog leather; however, he had not prepared (tanned) or used hides himself. Seventy-one per cent said their farm workers consumed the offal, particularly the head, liver, and kidneys.

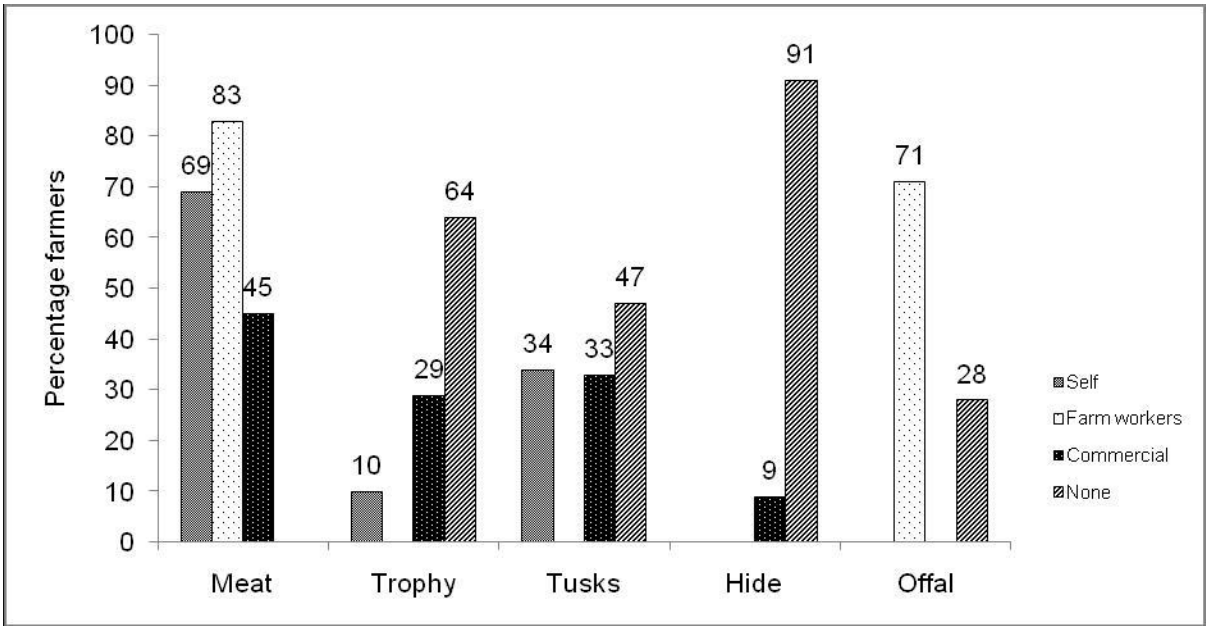

Figure 14: Utilization of warthogs culled from lands of farmers in the Northern Cape province of South Africa (from surveys conducted Jun–Oct 2012).

Seventy-five per cent of farmers were of the opinion that warthogs have indirectly resulted in livestock and game animal losses—the main reason being the damage caused to fences that allow predators to gain access to these animals. Animals also sometimes get stuck in warthog burrow openings and starve (especially when lying down to calve). Other reasons given by farmers that may affect overall animal health included 1) the transmission of parasites (such as ticks), 2) direct physical harm inflicted on livestock (jabbing sheep with tushes), and 3) a decrease in carrying capacity of the farmers' land.

The majority (83%) of farmers indicated that warthog populations require active management at present, and of these, 64% proposed that warthogs should actively be hunted. However, the more negative the view a farmer held about warthogs, the less inclined they were to manage warthog populations on their farm by themselves ($F_{1,57} = 10.88$, $P < 0.01$). In response to the question of whether farmers thought warthogs have financial value, 81% said yes, discriminating among 4 categories: meat production (78%), hunting (71%), eco-tourism (24%), and aesthetics (22%). Aesthetics refers to the notion that farmers themselves feel warthogs contribute to the beauty of natural environment. The majority (80%) indicated that they would be more likely to utilize the meat if presented with information on its nutritional profile. Older farmers ($\bar{x}$ age = 59 yr) were more likely than younger farmers ($\bar{x}$ age = 47 yr) to indicate that warthogs have no economic value whatsoever ($F_{9, 285}$ = 3.18, P = 0.01). Two farmers mentioned that other products (such as products made from the tail, hide, or tushes) may also have financial value. Farmers willing to manage the warthog cited its potential as an income-generating species for hunting and meat as the main motivation. Of the 19% that said warthogs have no financial value, 15% were livestock farmers and 4% were game farmers. Reviewing the personal profiles of the 4% indicated that their game farms were for personal recreational use and were not commercially orientated. Despite acknowledging that warthogs may have financial value, 15% of respondents maintained that they would not actively manage warthogs for potential financial benefits.

Livestock farmers, as opposed to game farmers, tended to prefer the area without warthogs (χ^2_1 = 9.05, P = 0.003) and were more likely to advocate complete eradication (χ^2_1 = 3.70, P = 0.06), whereas managers differed from farmers and owners by preferring the area with warthogs (χ^2_2, = 9.71, P = 0.008), and by not supporting full eradication (χ^2_2, = 6.82, P = 0.03). Farmers with increased tenure length ($\bar{x}$ = 25 yr) were more likely to support full eradication ($F_{1, 57}$ = 5.24, P = 0.03). Finally, older farmers ($\bar{x}$ age = 53 yr) would prefer the area without warthogs ($F_{1, 57}$ = 5.78, P = 0.02), but were not more likely to advocate their complete eradication ($F_{1, 57}$ = 3.09, P = 0.08). Farmers were interested in learning about a variety of topics related to warthogs (Table 4). Farmers appeared to be most interested in the basic biology and ecology of warthogs (30.5%), whereas only 2 farmers were interested in knowing the actual extent of damages caused by warthogs.

Table 4: Information regarding introduced warthogs that was indicated to be of interest by farmers (n = 59) interviewed in the Northern Cape and Free State provinces of South Africa between June and October 2012.

Response	No. of responses
Behavior, including reproduction, diet, feeding habits, habitat use	18
Associated parasites and zoonotic diseases	11
Meat utilization and production	6
Anything	6
Alternative management strategies	5
Effective management strategies	4
Current distribution of warthogs in South Africa	3
Actual extent of damages caused	2

5 Discussion

Although it was not within the scientific scope of this study to determine whether common warthogs are invasive to the region, they can be considered as such because of their extra-limital status and the negative impacts experienced by farmers as found in this study. Nyafu (2009) classified introduced populations in the Eastern Cape as invasive. There are currently no actual data available on warthog numbers in the region, while the overall population size in southern Africa (Angola, Zambia, Tanzania, and southward) has been estimated at approximately 250,000 (Cumming, 1999). Subpopulations are widespread across South Africa and likely increasing because of the continued expansion of game ranching. Furthermore, there are very limited data available on the damage caused by warthogs and the associated ecological and economic implications. The game ranching industry is governed by the Department of Environmental Affairs (DEA), which is currently in the process of amending national legislation in order to steer the industry in a more conservation-orientated direction, and DEA is still unsure how the new legislation will affect the industry, including the general translocation and management of game species on ranches (DEA, 2015). Current legislation does not provide guidance as to how introduced warthogs should or could be managed, and the free-roaming nature of warthogs further complicates proposed policy-making and management implications.

The damage caused to fences was the major concern to farmers because these openings allow previously excluded predators to gain access to vulnerable livestock, while smaller species (such as sheep or springbok [*Antidorcas marsupialis*]) are sometimes able to escape enclosures through these openings (Bothma & Du Toit, 2010). Prior to warthog introduction, electrical fencing had been hugely successful in managing the movements of black-backed jackals and caracals (Heard & Stephenson, 1987). According to conservative estimates, the average South African farmer loses 6.35% per annum of their small livestock flock to predation by black-backed jackals and caracals, which amounted to approximately 8.1 million animals lost to predation in the Northern Cape and 6 million in the Free State province in 2010 (De Wet, 2010). There are insufficient data on game animal losses to these predators, but black-backed jackals have been observed to hunt small ungulates such as springbok (<50 kg), fawn of larger ungulates (>50 kg), and on occasion large adult ungulates (Kamler, Foght, & Collins, 2010, Kamler. Klare, & Macdonald, 2012).

Maintaining the integrity of fences is therefore a priority for farmers, but can be compromised by the presence of the introduced warthog. Three farmers interviewed in this study have abandoned their sheep farming enterprises, because in their opinion, warthogs make predator management impossible and the losses to predation are deemed unacceptable. One small livestock farmer revealed that they suspected an adult male warthog was preying upon newborn lambs on their farm, and after killing the animal they found body parts of lambs in its stomach. Warthogs have rarely been recorded to actively hunt–prey on live animals (Roberts, 2012), but Choquenot, Lukins, & Curran (1997) found feral pigs to prey on newborn lambs in Western Australia.

Although the majority of farmers interviewed were not primarily crop farmers, all farmers who practiced some form of crop production noted the damage caused by warthogs. Warthogs may pose a significant threat to crop production because they are known crop raiders in their natural distribution range, most notably of maize (Weladji & Tchamba, 2003). The common warthog is considered a hyper-grazer, so it is clear that more research is required to determine their reliance on crops such as maize where these crops are available, or in the circumstance that natural grazing material is insufficient. However, many disparities exist between farmers' perceptions of, and actual, crop damage (McIvor & Conover, 1994, Wywialowski, 1994, Wang & Curtis, 2006). The main concern for farmers regarding the impact on the veld and soil systems was the rooting behavior warthogs use while foraging. Rooting by feral pigs essentially reduces vegetation cover and increases soil exposure and aeration (Husheer, Coomes, & Robertson, 2003, Barrios-Garcia, Classen, & Simberloff, 2014). Smit (2014) argued that their rooting is a high-impact form of veld degradation, although no studies have attempted to actually quantify the impact of their rooting.

Both livestock and game farmers were increasingly negative toward warthogs concerning their impact on the natural environment, but livestock farmers were more negative concerning the impacts on the agricultural environment. It is possible that livestock farmers are less tolerant of the damage caused to fences, water structures, and crops, but this is speculation because tolerance to damage was unfortunately not measured in this study. However, the overall tolerance of livestock farmers with regard to warthogs can possibly be inferred from the farmers' tendency to support eradication and to prefer the area without warthogs.

Overall, farmers who practiced no form of management tended to be more positive, while increasingly negative farmers were more likely to opportunistically hunt warthogs on their farms. Farmers referred to this type of hunting as 'shoot-on-sight,' which occurs when a farmer encounters a warthog on their land and they have their rifle on hand. It is similar to how they respond when encountering other so-called damage-causing species, notably jackals and caracals. The shot is taken hastily (sometimes while the animal is running), and the shot may be misplaced, which could result in the animal suffering or in a tainted carcass. 'Shoot on sight' satisfies the immediate need to exercise some form of control, but can be considered a temporary measure for unethical and ineffective population control. For example, the excessive hunting of jackals and caracals appears to be more costly and less effective in reducing depredation than are nonlethal control methods (McManus, Dickman, Gaynor, Smuts, & Macdonald, 2014), and has not allowed farmers to control the species or reduce the associated depredation. According to Thorn, Green, Dalerum, Bateman, & Scott (2012), social and environmental factors, rather than actual economic losses, appear to drive human–carnivore conflict among farmers in South Africa. This could possibly be the same for warthogs.

A small number of livestock farmers have resorted to using traps such as gin, spring, or trip-wire traps. Trip-wire traps are homemade devices, wherein a steel pipe is loaded with a shotgun shell and fixed to a fence where the problem animals move through, with a trip wire on the ground that releases a firing pin when touched. These traps are extremely dangerous and have a high percentage 'by-kill' because they are activated indiscriminately by any animal passing through. Warthogs caught in gin traps usually die from starvation and/or exposure, and not only does the animal experience prolonged suffering prior to death, but this also renders the carcasses unsuitable for utilization.

Hunting is commonly employed to control ungulate species because it is considered simple and effective, with the potential of providing economic benefits including meat production (Parkes & Murphy, 2003). The problem with hunting (by humans) is that it is typically biased by timing of hunting, and by age and sex of the targeted animal, which has undesirable effects on population dynamics of ungulates with stable age–sex structures. Indeed, studies have found that heavily hunted feral pig populations have an earlier onset of oestrus, earlier delivery dates, and faster generation times (Gamelon et al. 2011, Servanty et al. 2009, 2011), which increases productivity and recruitment. Festa-Bianchet (2008) advocated that hunting as an artificial management approach should attempt to mimic natural mortality, which requires a sound understanding of a species' population dynamics and interaction with the environment. It has been suggested for feral pigs that hunters focus their efforts on piglets and juveniles, and adult females in general, for effective population reduction and control (Bieber & Ruf, 2005, Servanty et al., 2011, Gamelon et al., 2012, Keuling et al., 2013). This might be difficult to achieve because younger individuals are smaller and less conspicuous, form smaller targets, and generally illicit sympathy from hunters (Festa-Bianchet, 2008, Keuling et al., 2013).

A number of increasingly negative farmers were still not willing to actively manage warthogs through hunting. The major reasons for the lack of utilization (in descending order) were that farmers 1) have more important activities to focus on concerning their agricultural practices, 2) do not have the facilities or labor force to hunt and process warthogs on a regular basis, and 3) believe no formal market exists that would encourage meat production and utilization. Even if such a market did exist and provided viable financial returns, a number of respondents still maintained they would not actively manage warthogs for financial gain. Here, it is suggested that young, game farmers be targeted as enforcers of sustainable hunting efforts for population control and damage mitigation, while educational efforts attempt to increase tolerance toward warthog damages among older, livestock farmers. Increased tolerance might effectively change negative attitudes and encourage sustainable utilization.

If the hunting of warthogs and subsequent processing of meat for commercial consumption can be facilitated, a commercial supply chain could be established that could benefit farmers and local communities and contribute toward local game-meat production. Although the idea of promoting human consumption of nonnative species as a means of control has previously been suggested (Roman, 2005), Nuñez, Kuebbing, Dimarco, and Simberloff (2012) debated that this approach should be carefully evaluated because it can create a market that must be sustained, facilitate the expansion of invasive populations, or promote further introductions. In certain cases the ecological and socio-economic conditions required for eradication of a pest species as set out by Bomford and O'Brian (1995) might not be present, and active control would be required to control population growth and dispersal (Hone, 2002).

Combining hunting and other control methods may further increase population control and mitigate damages. Some alternative ideas for managing warthogs and/or their impacts suggested by farmers include the use of reinforced fences, permanent through-ways in fences through which warthogs can move, and baited cage-traps to catch warthogs. Reinforced fences can limit wildlife movement and damage to crops, but the associated costs can be extremely high (Reidy Campbell, & Hewitt, 2008). Schumann, Schumann, Dickman, and Watson (2006) tested the use of swing gates in Namibia and found that warthogs, porcupines (*Hystrix africaeaustralis*) and aardvark (*Orycteropus afer*) readily use these gates while predators tended to avoid them. It was not determined whether small livestock or game animals could also move through these through-ways, and further investigation is required before it is suggested as a damage mitigation method. Lastly, farmers who used cages experienced varying levels of success; however, the specifications of cages, baiting, and placement methods differ, so further investigation would be useful.

5.1 Management Implications

Regardless of the many disparities between perceived and actual wildlife damage, farmers' perceptions of wildlife damage influences their attitudes and responses toward wildlife and should be addressed in order to mediate conflicts. Despite the small sample size and possible sources of bias, our study provides some of the first quantitative information on the interactions between farmers and introduced warthogs in South Africa, and expands the known distribution of the common warthog in the country. Warthogs appear to have a notable impact on the natural and agricultural environment, which influences farmers' attitude and behavior toward warthogs, resulting in farmers' use of unsustainable and unethical management practices. The actual extent of warthog impact warrants further investigation because there is limited information on this in the literature. Eradication of the species is unlikely; therefore, formal management should be employed to control population numbers and reduce the levels of damage experienced. Providing farmers with an incentive to manage warthogs might work toward changing negative attitudes, discouraging the use of opportunistic hunting, and promoting sustained management.

Regulated and informed hunting can be proposed as the best method for control because it can provide financial returns and contribute to the game-meat industry in the country. Incorporating basic biological and ecological information on warthogs would help facilitate the hunting effort (e.g., being aware of their daily behavior patterns, reproductive seasons, habitat use, etc.) Farmers can also acquiring relevant information about the warthog populations found on their land (e.g., the location of used burrows, water holes, or regularly frequented grazing areas). Finally, farmers and hunters could create networks of farms on which warthogs are regularly hunted, while hunters could establish connections with game-meat abattoirs and butcheries to directly supply warthog meat to the commercial production chain.

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Supporting material

Additional supporting material may be found in the online version of this article at the publisher's web-site. This includes section C and D of the survey questionnaire as mentioned in the Methods section.

7 References

Acocks, J. P. H. (1988). Veld types of South Africa. Memoirs of the Botanical Survey of South Africa. No 57. Pretoria, South Africa: Government Printer

Babbie, E. & Mouton, J. (2001). *The practice of social research*. Cape Town, South Africa: Oxford University Press.

Barnes, J. I. & De Jager, J. L. V. (1996). Economic and financial incentives for wildlife use on private land in Namibia and the implications for policy. South African Journal of Wildlife Research, 26, 37-46. Retrieved from: http://content.ajarchive.org/cdm4/document.php?CISOROOT=/03794369&CISOPTR=2157&REC=1.

Barrios-Garcia, M., Classen, A., & Simberloff, D. (2014). Disparate responses of above-and belowground properties to soil disturbance by an invasive mammal. *Ecosphere*, *5*, 1–13. Retrieved from http://www.esajournals.org/doi/abs/10.1890/ES13-00290.1

Bengsen, A. J., Gentle, M. N., Mitchell, J. L., Pearson, H. E., & Saunders, G. R. (2014). Impacts and management of wild pigs *Sus scrofa* in Australia. *Mammal Review*, *44*, 135–147. doi:10.1111/mam.12011

Benson, D. E. (1991). Values and management of wildlife and recreation on private land in South Africa. *Wildlife Society Bulletin, 14*, 497-510. Retrieved from: http://www.jstor.org/stable/3782165.

Bieber, C., & Ruf, T. (2005). Population dynamics in wild boar Sus scrofa: Ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *Journal of Applied Ecology*, *42*(6), 1203–1213. doi:10.1111/j.1365-2664.2005.01094.x

Bomford, M., & O'Brien, P. (1995). Eradication or control for vertebrate pests? *Wildlife Society Bulletin*, *23*(2), 249–255. Retrieved from http://www.jstor.org/stable/3782799

Bothma, J. du P., & Du Toit, J. G. (2010). *Game ranch management*. Pretoria, South Africa: Van Schaik.

Castley, J. G., Boshoff, A. F. & Kerley, G. I. H. (2001). Compromising South Africa's natural biodiversity – inappropriate herbivore introductions. *South Africa Journal of Science, 97*, 344–348. Retrieved from http://reference.sabinet.co.za/webx/access/electronic_journals/sajsci/sajsci_v97_n9_a4.pdf.

Choquenot, D., Lukins, B., & Curran, G. (1997). Assessing lamb predation by feral pigs in Australia's semi-arid rangelands. *Journal Applied Ecology, 34,* 1445–1454.

Chown, S. L., Spear, D., Lee, J. E. & Shaw, J. D. (2009). Animal introductions into southern systems: lessons for ecology and for policy. *African Zoology, 44*, 248-262. doi: 10.3377/004.044.0213.

Clout, M., & Russell, J. (2007). The invasion ecology of mammals: a global perspective. *Wildlife Research*, *35*, 180–184. Retrieved from http://www.publish.csiro.au/paper/WR07091

Conover, M. R. (1998). Perceptions of American agricultural producers about wildlife on their farms and ranches. *Wildlife Society Bulletin, 26*, 597-604. Retrieved from http://www.jstor.org/stable/3783775.

Cousins, J. A., Sadler, J. P. & Evans, J. (2010). The challenge of regulating private wildlife ranches for conservation in South Africa. Ecology and Society, 15, 28. Retrieved from http://www.ecologyandsociety.org/vol15/iss2/art28/.

Cumming, D. H. M. (1999). Study on the development of Transboundary Natural Resource Management areas in southern Africa. Environmental context: Natural Resources, land use and conservation. Washington, D.C., USA: Biodiversity Support Program,.

De Wet, P. (2010). Predation management forum: norms and standards for the management of damage-causing animals in South Africa. Meeting of the Parliamentary Monitoring Group, Cape Town, South Africa. Retrieved from http://www.pmg.org.za/report/20101102-norms-and-standards-management-damage-causing-animals-south-africa.

Department of Agriculture, Forestry and Fisheries (DAFF). (2013). *South African Yearbook 2012/13: Agriculture, Forestry and Fisheries*. In A. Vermeulen (Ed.). Department of Agriculture, Forestry and Fisheries (pp 44–82). Pretoria, South Africa. Retrieved fromhttp://www.gcis.gov.za.

Department of Environmental Affairs (DEA). (2015). National Environmental Management: Biodiversity Act, 2004 (Act No. 10 of 2004). Norms and standards for the translocation of indigenous species in South Africa. Volume 595, Government Gazette (38395) (pp 1–16). Government Printer: Pretoria, South Africa. Retrieved from www.gpwinline.co.za.

Festa-Bianchet, M. (2008). Ecology, evolution, economics, and ungulate management. In T. E. Fulbright and D. G. Hewitt (Eds.), *Wildlife science: linking ecological theory and management applications* (pp 183–202). Boca Raton, Florida, USA: CRC

Forsyth, D. M., & Duncan, R. P. (2001). Propagule size and the relative success of exotic ungulate and bird introductions to New Zealand. *The American Naturalist*, *157*, 583–95. doi:10.1086/320626

Fraser, K. W., Cone, J. M., & Whitford, E. J. (2000). A revision of the established ranges and new populations of 11 introduced ungulate species in New Zealand. *Journal of the Royal Society of New Zealand*, *30*, 419–437. doi:10.1080/03014223.2000.9517633

Gamelon, M., Besnard, A., Gaillard, J., Servanty, S., Baubet, E., Brandt, S., & Gimenez, O. (2011). High hunting pressure selects for earlier birth date: Wild boar as a case study. *Evolution*, *65*, 3100–3112. doi:10.1111/j.1558-5646.2011.01366

Goodman, L. A. (1961). Snowball sampling. *Annals Mathematical Statistics*,*32*, 148-170. doi: 10.1214/aoms/1177705148.

Heard, H., & Stephenson, A. (1987). Electrification of a fence to control the movements of black-backed jackals. Suid Afrika Tydskrif van Natuurnavorsing 17, 20–24.

Higginbottom, K. & King, N. (2006). The live trade in free-ranging wildlife within South Africa, and implications for Australia. Report for the Rural Industries Research and Development Corporation. ISBN 1 74151 309 X ISSN 1440-6845.

Hone, J. (2002). Feral pigs in Namadgi National Park, Australia: Dynamics, impacts and management. Biological Conservation, 105, 231–242. doi:10.1016/S0006-3207(01)00185-9

Husheer, S. W., Coomes, D. A., & Robertson, A. W. (2003). Long-term influences of introduced deer on the composition and structure of New Zealand Nothofagus forests. *Forest Ecology and Management, 181,* 99–117.

Kamler, J. F., Foght, J. L., & K. Collins. (2010). Single black-backed jackal (*Canis mesomelas*) kills adult impala (*Aepyceros melampus*). *African Journal of Ecology, 48,* 847–848.

Kamler, J. F., Klare, U., & Macdonald, D. W. (2012). Seasonal diet and prey selection of black-backed jackals on a small-livestock farm in South Africa. *African Journal of Ecology, 50,* 299–307.

Keuling, O., Baubet, E., Duscher, A., Ebert, C., Fischer, C., Monaco, A., … Thurfjell, H. (2013). Mortality rates of wild boar Sus scrofa L. in central Europe. *European Journal of Wildlife Research*, *59*, 805–814. doi:10.1007/s10344-013-0733-8

Lowney, M., Schoenfeld, P., Haglan, W., & Witmer, G. (2005). Overview of impacts of feral and introduced ungulates on the environment in the eastern United States and Caribbean. In D. L. Nolte and K. A. Fagerstone (Eds). Proceedings of the 11th wildlife damage management conferences (pp 64–81). Retrieved from http://digitalcommons.unl.edu/icwdm_wdmconfproc/88/.

Luxmoore, R. (1985). Game farming in South Africa as a force for conservation. *Oryx, 19*, 225-234. doi: 10.1017/S0030605300025667.

Maciejewski, K., & Kerley, G. I. H. (2014). Understanding tourists' preference for mammal species in private protected areas: is there a case for extralimital species for ecotourism? *PloS One*, *9*(2), e88192. doi:10.1371/journal.pone.0088192

Madden, F. (2004). Creating Coexistence between Humans and Wildlife: Global Perspectives on Local Efforts to Address Human–Wildlife Conflict. *Human Dimensions of Wildlife*, *9*, 247–257. doi:10.1080/10871200490505675

Mason, D. R. (1982). *Studies on the biology and ecology of the warthog Phacochoerus aethiopicus sundevalli Lönnberg, 1908 in Zululand, South Africa*. Dissertation, University of Pretoria, Pretoria, South Africa.

McIvor, D., & Conover, M. (1994). Perceptions of Farmers and Non-Farmers toward Management of Problem Wildlife. *Wildlife Society Bulletin*, *22*, 212–219.

McManus, J. S., Dickman, A. J., Gaynor, D., Smuts, B. H., & Macdonald, D. W. (2014). Dead or alive? Comparing costs and benefits of lethal and non-lethal human–wildlife conflict mitigation on livestock farms. *Oryx*, 1–9. doi:10.1017/S0030605313001610

Nuñez, M. A., Kuebbing, S., Dimarco, R. D., & Simberloff, D. (2012). Invasive Species: to eat or not to eat, that is the question. *Conservation Letters*, *5*(5), 334–341. doi:10.1111/j.1755-263X.2012.00250.x

Nyafu, K. (2009). *Warthogs as an introduced species into the Eastern Cape*. Unpublished MSc thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

Parkes, J., & Murphy, E. (2003). Management of introduced mammals in New Zealand. *New Zealand Journal of Zoology*, *30*, 335–359. Retrieved from http://www.tandfonline.com/doi/abs/10.1080/03014223.2003.9518346

Penzhorn, B. L. (1971). A summary of the reintroduction of ungulates into South African National Parks (to 31 December 1970). *Koedoe, 14,* 145–159.

Stellenbosch University http://scholar.sun.ac.za

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., … Tsomondo, T. (2001). Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environment*, *84*, 1–20. doi:10.1016/S0167-8809(00)00178-X

Reidy, M. M., Campbell, T. A. & Hewitt, D. G. (2008). Evaluation of electric fencing to inhibit feral pig movements. *The Journal of Wildlife Management*, *72*, 1012-1018. doi: 10.2193/2007-158.

Roberts, B. A. (2012). An attack by a warthog Phacochoerus africanus on a newborn Thomson's gazelle *Gazella thomsonii*. *African Journal of Ecology*, *50*, 507–508. doi:10.1111/j.1365-2028.2012.01344.x

Roman, J. (2005, September). We shall eat them on the beaches ; We've a talent for eating species to extinction, so why not put it to good use for a change. *New Scientist*, 41–44. Retrieved from http://www.newscientist.com/article/mg18725161.500-how-to-defeat-and-eat-invading-species.html.

Rutherford, M. C. & Westfall, R. H. (1994). *Biomes of Southern Africa: An Objective Categorization*. (2nd ed.). Memoirs of the Botanical Survey of South Africa 63. Pretoria, South Africa: National Botanical Institute.

Sabrina, S., Jean-Michel, G., Carole, T., Serge, B., & Eric, B. (2009). Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. *The Journal of Animal Ecology*, *78*, 1278–90. doi:10.1111/j.1365-2656.2009.01579.x

Sabrina, S., Jean-Michel, G., Carole, T., Serge, B., & Eric, B. (2009). Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. *The Journal of Animal Ecology*, *78*, 1278–90. doi:10.1111/j.1365-2656.2009.01579.x

Schumann, M., Schumann, B., Dickman, A., & Watson, L. H. (2006). Assessing the use of swing gates in game fences as a potential non-lethal predator exclusion technique. *South African Journal of Wildlife Research*, *36*, 173-181. Retrieved from http://content.ajarchive.org/cdm4/document.php?CISOROOT=/03794369&CISOPTR=1271&REC=11.

Servanty, S., Gaillard, J. M., Ronchi, F., Focardi, S., Baubet, É., & Gimenez, O. (2011). Influence of harvesting pressure on demographic tactics: Implications for wildlife management. *Journal of Applied Ecology*, *48*, 835–843. doi:10.1111/j.1365-2664.2011.02017.x

Smit, Z. M. 2014. *The ecological planning of Doornkloof Nature Reserve*. Thesis, University of the Free State, Bloemfontein, South Africa.

Somers, M. J. (1992). The implications of social structure for the conservation and control of a warthog Phacochoerus aethiopicus population in the Andries Vosloo Kudu Reserve, Eastern Cape Province. Unpublished MSc thesis, University of Pretoria.

Spear, D. & Chown, S. L. (2009). The extent and impacts of ungulate translocations: South Africa in a global context. *Biological Conservation, 142*, 353–363. doi: 10.1016/j.biocon.2008.10.031.

Stankus, T. (2012). Razorbacks: Feral pigs as agricultural pests, disruptors of ecosystems, reservoirs of contagion, and favoured game for sport and subsistence hunters: A review of the literature, 2005-2011. *Journal of Agricultural and Food Information, 13,* 283-301. doi: 10.1080/10496505.2012.694270.

Thorn, M., Green, M., Dalerum, F., Bateman, P. W., & Scott, D. M. (2012). What drives human–carnivore conflict in the North West Province of South Africa? *Biological Conservation*, *150*, 23–32. doi:10.1016/j.biocon.2012.02.017

Treves, A., Wallace, R. B., Naughton-Treves, L., & Morales, A. (2006). Co-managing human–wildlife conflicts: A review. *Human Dimensions of Wildlife*, *11*(6), 383–396. doi:10.1080/10871200600984265

Van der Merwe, P. & Saayman, M. (2004). *Managing game farms from a tourism perspective*. Potchefstroom, South Africa: Leisure C Publications.

Vercammen, P. & Mason, D. R. (1993). *The Warthogs* (P*hacochoerus africanus* and *P. aethiopicus*). In W. L. R. Oliver (Ed.), *Pigs, Peccaries, and Hippos: Status Survey and Conservation Action Plan* (pp. 75-84). Gland, Switzerland: IUCN/SSC Pigs and Peccaries Specialist Group. Retrieved from https://portals.iucn.org/library/efiles/edocs/1993-055.pdf.

Wang, S., & Curtis, P. (2006). Farmer perceptions of crop damage by wildlife in Jigme Singye Wangchuck National Park, Bhutan. *Wildlife Society Bulletin*, *34*, 359–365. doi:10.2193/0091-7648(2006)34[359:fpocdb]2.0.co;2

Weladji, R. B. & Tchamba, M. N. (2003). Conflict between people and protected areas within the Be´noue´ Wildlife Conservation Area, North Cameroon. *Oryx, 37*, 72-79. doi: 10.1017/S0030605303000140.

Wywialowski, A. P. (1994). Producers ’ perceptions of agricultural wildlife-caused losses. *Wildlife Society Bulletin*, *22*, 370–382.

Chapter 5

Carcass yield of common warthog (*Phacochoerus africanus*), influence of season and sex*

Abstract

The carcass yield and dress out percentage of the common warthog (*Phacochoerus africanus*) was investigated as influenced by season and sex. Season did not have a significant impact on the carcass weights ($P = 0.64$) and dress out percentages ($P = 0.28$) of adult warthogs (N = 46). Males (N = 21) had heavier carcass weights (35.24 kg ± 2.59) than females (N = 25) (27 kg ± 0.96) ($P = 0.03$) and had a higher dress out percentage (57.14% ± 0.91) than females (52.14% ± 0.91) ($P < 0.01$). Due to the imbalance in sampled populations age was not included as a variable in the final analyses. Warthogs have a favourable carcass yield and can be utilized for commercial game meat production.

Keywords: warthog, carcass, yield, dressed weight, season, sustainable utilization

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1 Introduction

The potential large-scale meat production from wild ungulates has received increased attention since the 1960's, largely due to the high biodiversity and wide-spread occurrence of ungulate species in South Africa (Carruthers, 2008, Hoffman & Cawthorn, 2012). Following the amendment of wildlife protection policies during the 1970's, wildlife protection and utilization on state-owned and private reserves and farms have increased significantly in the country (Luxmoore, 1985, Benson, 1991). The game farming industry has grown from 8.5% of the total land cover in South Africa utilized for game farming in 1993 to 16.8% in 2008 (Dry, 2012), and is recognized as one of the fastest growing agricultural enterprises in the country (Stroleny-Ford, 1990, NAMC, 2006). The term "game farming" rather than "game ranching" is used here to refer to the South African practice where certain wildlife species are maintained, either intensive or extensively, on fenced land for private or commercial purposes.

Currently, more than 12 000 game farms operate in South Africa with over 50% located in the Limpopo province (Dry, 2012). The wildlife industry generates revenue through eco-tourism, recreational (biltong)-and-trophy hunting, live trade and sales, taxidermy and meat production (Van der Merwe & Saayman, 2003, Cloete et al., 2007). In 2012 the industry contributed a total of R10 billion (Rand) to the country's GDP (Dry, 2012), and Saayman et al., (2011) estimated the total contribution made by "biltong"-hunters to the South African economy to be more than R6 billion. Springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus pygargus phillipsi*), impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*) and gemsbok (*Oryx gazella*) are the most popular species utilized by South Africans (Jansen van Rensburg, 1992, Hoffman et al., 2003, Hoffman et al., 2005b), while springbok, blesbok, impala and greater kudu are the major species exported for game meat (Hoffman, 2007).

During the six month hunting season, game meat contributes approximately 10% of red meat utilized per annum in South Africa, which was estimated at around 1 249 000 tons during 2011/2012 (Department of Agriculture, Forestry and Fisheries, DAFF, 2013). The South African government in collaboration with Wildlife Ranching South Africa (WRSA) is also in the process of implementing a national Game Meat Scheme that aims to promote and regulate the harvesting, production and retail of game meat for the local and international market (DAFF, 2012). This scheme will operate under the Meat Safety Act, 2000 (Act No. 40 of 2000).

Several southern African ungulate species have been investigated for their meat producing potential, of which include the gemsbok, impala, springbok, Burchell's zebra (*Equus quagga*), greater kudu, red hartebeest (*Alcelaphus buselaphus*), black wildebeest (*Connochaetes gnou*), blue wildebeest (*Connochaetes taurinus*), mountain reedbuck (*Redunca fulvorufula*) and blesbok (Huntley, 1971, Onyango et al., 1998, Hoffman, 2000, Van Zyl & Ferreira, 2004, Taylor et al., 2005, Mostert & Hoffman, 2007, Hoffman et al., 2005a, Hoffman et al., 2007, Hoffman et al., 2008a, Hoffman et al., 2008b, Hoffman et al., 2009a, Hoffman et al., 2009b, Hoffman et al., 2010, Hoffman et al., 2011). The common warthog (*Phacochoerus africanus*) is a species traditionally considered as "bushmeat" and has historically been hunted and consumed by rural communities throughout its large distribution range, which stretches from South Africa towards central and northern Africa, reaching Ethiopia in the east and Nigeria to Senegal in the west (Vercammen & Mason, 1993, Somers, 1997). In 2009 a total of 2049 warthogs were officially recorded as being hunted by international trophy hunters in South Africa which increased to 3 849 in 2013, making warthogs the 2nd most often trophy hunted in South Africa (Professional Hunters Association of South Africa (Professional Hunters Association of South Africa [PHASA], 2014). These numbers however do not represent all the warthogs hunted in the country as it is expected that the majority of recreational and damage control hunting remain unreported, while there are farmers who have reported to the authors that they cull on average over 700 per annum on their farm. Hunters will pay anything between R500 and R3500 for a warthog, depending on the trophy value of the animal (A. Barnard, pers. comm., 2013).

The meat production potential of the common warthog has only been briefly touched upon, with Crawford et al., (1970) describing the muscle and adipose lipids of warthogs, Somers (1992) reporting on carcass yields in the Andries Vosloo Koedoe Reserve, Eastern Cape, and Hoffman and Sales (2007) investigating the physical and chemical characteristics of warthog meat. Similar to other game species, warthogs have a high dressing percentage, low total intramuscular lipid content, high total protein and moisture content and a favourable fatty acid profile. Regardless of these findings, the meat from hunted carcasses is still relatively under-utilized by hunters and/or the commercial sector (Hoffman et al., 2005b). Encouraged formal utilization of the meat from both formal and informal harvesting may contribute to food security not only in South Africa but the African continent as a whole.

The common warthog has been introduced extra-limitally onto provincial and private lands in the Northern Cape, Eastern Cape and Free State provinces since the 1960's (H. Blom, pers. comm., 23 August 2013). Multiple introduction events coupled with a high reproduction rate has allowed warthogs to greatly expand their range and inhabit areas where they were historically absent (Grubb & D'Huart, 2010). The species has become a managerial problem in agricultural settings, as they are known to be agricultural pests (Mason 1982, Somers 1992, Vercammen & Mason, 1993, Nyafu, 2009). Farmers and land-owners are currently employing a shoot-on-sight strategy to control populations and mitigate negative impacts. While game farmers exploit the species for financial gain through hunting and tourism, crop and livestock farmers consider warthogs a damage-causing animal that incurs financial losses. The potential of the warthog as a meat producing animal contributes little to current utilization.

Although warthog meat has not always been considered as part of the formal game meat spectrum, it is becoming more widely known and accepted by modern consumers. Hoffman et al., (2005b) found warthog to be a game meat species regularly consumed in South Africa and South African restaurants. For any animal species to be utilized commercially, information on the yield and the factors that influence it are a prerequisite so as to calculate the economic feasibility for utilization of said species. The present investigation evaluated the yield and carcass morphology from warthogs culled in the Kimberley area during three culling events in 2011. The objective was to determine the carcass yield of warthogs as influenced by three parameters - season, age and sex, in light of promoting the species for commercial meat production in South Africa.

2 Methods

2.1 Study area

Free-roaming warthogs were culled on farms in the Northern Cape and Free State provinces, around the city of Kimberley (28° 44’ 31’ S, 24° 46’ 19’ E), South Africa. Kimberley has a continental climate with hot, wet summers and cold, dry winters. Frost during winter is not uncommon. Mean maximum monthly temperatures reach highs of 36.2°C in January (summer) and lows of 18.2°C in June (winter), and mean minimum monthly temperatures are highest in January (17.6°C) and lowest in July (2.7°C). Being situated in a summer rainfall region, mean precipitation rates are highest during March (73.66 mm) and lowest in June/July (7.4/7.3 mm), with an annual mean of 420.4 mm.

The area consists primarily of Kimberley Thornveld and Western Free State Clay Grassland type vegetation. The grassy, dwarf shrubland of the Kimberley Thornveld region is based largely on rocky, sandy soils, giving rise to mainly hemicryptophytes and chameaphytes (Rutherford & Westfall 1994). The grass-and-shrub layer is well developed or may be dominated by thorny shrubs, revealing large patches of uncovered soil. Overall, the region consists of fairly open shrubland dominated by species such as candle-thorn (*Acacia hebeclada),* sweet thorn (*A. karroo*), giraffe thorn (*Vachellia erioloba,* formerly *Acacia erioloba*), and umbrella thorn (*Vachellia tortilis,* formerly *Acacia tortilis).* Other dominant species include camphor bush (*Tarchonanthus camphorates),* karee tree (*Searsia lancea,* formerly *Rhus lancea*) and velvet raisin (*Grewia flava).* Dominant graminiods species include wool grass (*Anthephora pubescens),* thimble grass *(Fingerhuthia africana),* common finger grass *(Digitaria eriantha),* spear grass (*Heteropogon contortus),* silky bushman grass *(Stipagrostis uniplumis),* red grass *(Themeda triandra),* couch grass (*Cynodon dactylon)* and Lehmann's love grass *(Eragrostis lehmanniana)* (Mucina & Rutherford, 2006).

The Western Free State Clay Grasslands are known as the *Eragrostis obtusa/Eragrostis lehmanniana* grasslands (Cowling et al., 1997). The unit represents the drier areas of the grassland biome based largely on alluvial clay soils (Mucina & Ruherford, 2006). The vegetation composition is complex, since it borders on and consists of species from the Kalahari Thornveld as well as dwarf shrubs and grass species typical of the grassland biome. Species characteristic of the region include *Eragrostis* species, *T. triandra, S. uniplumis* and *F. africana*.

Farms (N=12) over a surface area of 2 000 km^2 were identified that would possibly allow the culling of warthogs on the properties. Farmers/land-owners were contacted and the purpose of the research was explained, after which permission was asked to cull warthogs on their properties. Farmers were assured that culling would be conducted as ethically as possible, and hunters with sufficient experience would use their own registered weapons to cull the animals.

2.2 Harvesting, slaughtering and physical measurements

A total number of 58 warthogs were shot using single shot bolt action rifles (Ethical clearance number: 11LV_HOF02). The warthogs were shot as and when sighted without any bias towards sex or age. Nineteen warthogs were shot in March 2011 (representing autumn), 18 in June 2011 (representing winter) and 21 in October 2011 (representing spring). The composition of each group regarding age and sex is depicted in Table 1. Other studies used tusk protrusion and molar eruption as the basis for classifying age classes, however since the data capturing team was not confident with this method, weight and general tusk protrusion was used instead as a visual tool for age classification (Mason, 1984). Animals weighing less than 35 kg, with no tusk protrusion past the flanges of the lips were classified as juveniles, and all other animals classified as mature adults.

Immediately after shooting, the animals were exsanguinated by thoracic sticking, transported to a slaughter facility, weighed and dressed. The dead weight of the animal was defined as the total weight of the animal (minus the blood lost during exsanguination), while carcass weight refers to the weight after the animal has been dressed. Dressing entailed the removal of the head, feet and skin. The head was removed by making a horizontal cut between the axis and atlas bones of the neck vertebrae. The front pair of feet was removed by making a horizontal cut across the radius and ulna bones directly above the carpal joint, while the back pair was removed by cutting through the tarsal and tibia bone directly below the point where the fibula fuses with the tibia. The skin was removed by starting at the anus and working towards the neck area, while attempting to leave as much subcutaneous fat on the carcass as possible. After evisceration the carcass was washed, allowed to drip dry for ± 20 minutes before being weighed again. The hot carcass weight was then measured. The head, feet and skin were weighed separately.

After evisceration, the total intestinal contents (large and small intestines) of each animal were weighed separately. This included the heart, liver, lungs (with trachea and lung pipes), spleen, kidneys (as a pair), stomach, and the testes (as a pair) if the animal were male. If a female was pregnant, the foetuses were removed, sexed and weighed individually. The weight of the foetuses was subtracted from the dead weight of pregnant females to calculate carcass weight and dress out percentage.

Table 5. Age and sex group distribution of common warthogs (N=58) sampled in three different seasons.

	Autumn		Winter		Spring		
Sex	Male	Female	Male	Female	Male	Female	Total
Adult	3	9	13	4	5	12	46
Juvenile	5	2	0	1	2	2	12
Total	8	11	13	5	7	14	58

2.3 Statistical analysis

The data was analysed using Statistica 12 (Statistica, 2013). Analysis of variance (ANOVA's) with the main effects sex and season was performed. The model for the experimental design is indicated by the following equation:

$$y_{ij} = \mu + s_i + g_k + s_i g_k + \varepsilon_{ik}$$

The terms are defined as: the overall mean (μ), the effect of season (s_i), the effect of sex (g_k), the interactions between the main effects ($s_i g_k$) and the error associated with the effects of season and sex (ε_{ik}). The LS means and Fisher's LSD tests were used to compare levels within factors. P-values smaller than 0.05 were considered significant ($P < 0.05$).

3 Results

The age and sex distribution of sampled warthogs ($N = 58$) are presented in Table 1. Due to the imbalance in sampled populations, age as a variable was omitted and only the effect of season and gender on adult warthog carcass yield and composition was determined ($N = 46$). As season and sex had no interaction ($P > 0.05$), the data was analysed and presented separately according to the main effects. A descriptive summary of the data on juvenile warthogs is presented at the end of the Results section.

3.1 Season

Season had no significant effect on dead, carcass and dressed weight, as well as dress out percentage (Table 2). Season significantly influenced the percentage skin ($P < 0.01$) and trotters ($P = 0.01$), with the skin from warthogs culled during autumn contributing a smaller percentage to their total body weight, and warthogs from winter having the heaviest trotters/body weight. The total intestinal contribution to body weight also differed between seasons, being the lowest during winter and highest in spring ($P = 0.06$). Of all the organs, only the spleen ($P < 0.01$) and kidneys ($P = 0.01$) differed significantly among seasons.

The adjusted carcass weight and adjusted dress out percentage were also calculated with the head, skin and trotters weights included (Table 2) (as done for commercially slaughtered pigs). The adjusted dress out percentage differed at the 10% significance level ($P = 0.09$) between seasons. Warthogs culled during winter had the highest adjusted dress out percentage.

Table 6. The average (± SE) carcass yields and dress out percentages of adult common warthogs culled in three seasons.

Variable	Autumn (N=12)	Winter (N=17)	Spring (N=17)	P-value
Dead weight (kg)	53.36 ± 2.98	60.87 ± 4.54	53.55 ± 3.78	0.76
Carcass weight (kg)	28.35 ± 1.92	34.73 ± 2.65	28.74 ± 2.34	0.64
Dress out (%)*	54.10 ± 0.85	56.56 ± 0.95	52.47 ± 1.56	0.28
Skin (%)*	6.21 ± 0.12[a]	7.81 ± 0.36[b]	7.36 ± 0.24[ab]	<0.01
Trotters (%)*	1.34 ± 0.06[a]	1.60 ± 0.07[b]	1.29 ± 0.04[a]	0.01
Head (%)*	12.24 ± 0.24	12.61 ± 0.30	12.21 ± 0.46	0.81
Total intestine (%)*#	23.26 ± 0.84[ab]	21.11 ± 1.30[b]	26.19 ± 1.40[a]	0.06
Heart (%)*	0.44 ± 0.03	0.54 ± 0.03	0.50 ± 0.04	0.23
Liver (%)*	1.44 ± 0.07	1.37 ± 0.04	1.49 ± 0.06	0.23
Lungs (%)*	0.75 ± 0.08	0.76 ± 0.05	0.77 ± 0.08	0.89
Spleen (%)*	0.12 ± 0.01[a]	0.17 ± 0.01[b]	0.11 ± 0.01[a]	<0.01
Kidneys (%)*	0.28 ± 0.02[a]	0.28 ± 0.01[a]	0.25 ± 0.02[b]	0.01
Stomach (%)*#	3.73 ± 0.68	3.63 ± 0.54	2.60 ± 0.60	0.24
Adjusted carcass weight (kg)#	40.57 ± 3.27	49 ± 4.10	44.34 ± 4.47	0.72
Adjusted dress out (%)##	74.17 ± 0.48[a]	79.21 ± 1.14[b]	74.89 ± 1.16[a]	0.09

*Variables were calculated as a percentage of dead weight.
*#Total intestine weight and stomach weight was measured as full intestine and full stomach weight.
abcValues with different superscripts in the same row are significantly different.
#Adjusted variables were calculated with head, skin and trotter weights included.
##Adjusted variables were calculated as percentage adjusted carcass weight of dead weight.

3.2 Sex

Sex had a significant effect on carcass weight ($P = 0.03$) and dress out percentage ($P < 0.01$), with males having on average heavier carcass weights and a higher dress out percentage than females (Table 3). The total contribution made by the skin ($P < 0.01$) and head ($P = 0.03$) to total body weight was also higher in males than females. The kidneys were the only organ that differed between males and females ($P < 0.01$). The adjusted carcass weight and adjusted dress out percentage were also calculated with the head, skin and trotters included (Table 3), as done for the seasonal analysis (Table 2). The adjusted carcass weight differed between male and female warthogs ($P = 0.02$), but not the adjusted dress out percentage (P = 0.41).

Testes made a 0.24% contribution to the total body weight of males. The testes weights were not analysed according to season as the testes from only one male was collected during the autumn sampling period. A total of eight female warthogs culled during the spring season were found to be pregnant, with an average litter size of 3.9 (± 0.3) piglets. The highest contribution made to total body weight by a litter was 6.08% (4 piglets with an average weight of 910g) and the lowest was 1.97% (3 piglets with an average weight of 327g). All the pregnant females were adults.

Table 7: The average (± SE) carcass yields and dress out percentages of adult male and female common warthogs.

Variable	Male (N=21)	Female (N=25)	P-value
Dead weight (kg)	61.23 ± 4.55	51.95 ± 1.69	0.15
Carcass weight (kg)	35.24 ± 2.59	27 ± 0.96	0.03
Dress out (%)*	57.16 ± 0.91	52.14 ± 0.91	<0.01
Skin (%)*	7.18 ± 0.27	7.47 ± 0.33	<0.01
Trotters (%)*	1.52 ± 0.08	1.37 ± 0.04	0.66
Head (%)*	12.91 ± 0.31	11.99 ± 0.23	0.03
Total intestine (%)*#	22.05 ± 1.32	23.52 ± 0.99	0.61
Heart (%)*	0.52 ± 0.03	0.48 ± 0.02	0.95
Liver (%)*	1.40 ± 0.05	1.43 ± 0.04	0.47
Lungs (%)*	0.74 ± 0.06	0.78 ± 0.05	0.50
Spleen (%)*	0.15 ± 0.01	0.13 ± 0.01	0.29
Kidneys (%)*	0.32 ± 0.01	0.24 ± 0.01	<0.01
Stomach (%)*#	3.13 ± 0.38	3.48 ± 0.53	0.30
Adjusted carcass weight (kg)#	52.03 ± 4.30	39.36 ± 1.25	0.02
Adjusted dress out (%)##	78.71 ± 1.18	75.07 ± 0.83	0.41

*Variables were calculated as a percentage of dead weight.
*#Total intestine weight and stomach weight was measured as full intestine and full stomach weight.
#Adjusted variables were calculated with head, skin and trotter weights included.
##Adjusted variables were calculated as percentage adjusted carcass weight of dead weight.

3.3 Descriptive data of juvenile warthogs

The juvenile group consisted of five female juveniles and seven male juveniles, and thus due to sample size limitations, no statistical comparisons were made (Table 1). Male juveniles tended to have a heavier dead weight (29.5kg ± 3.0) than female juveniles (19.3kg ± 3.1), but very similar dress out percentages (48.7% ± 1.7, and 48.2% ± 4.2 respectively). The contribution of total intestinal weight to body weight was higher in female juveniles (27.5% ± 2.9) than males (24.5% ± 0.6), but the rest of the carcass composition was very similar. Testes made a 0.1% (± 0.01) contribution to total weight in males. No juvenile females were found to be pregnant.

4 Discussion

4.1 General

It should be noted that harvested wild ungulates develop under variable conditions and sampled populations may vary greatly in composition. Species, geographic range, season, age and sex influence the carcass yields and dress out percentages of wild ungulates to varying degrees (Talbot et al., 1965, Skinner 1970, Huntley 1971, Von la Chevallerie 1971, Hoffman 2000, Taylor et al., 2005, Hoffman 2007, Hoffman et al., 2009a, b). Growth and development is influenced both by genetic and environmental qualities which determine muscle acquisition, fat deposition, bone formation, and possible sexual dimorphism, all these factors varying periodically. Body weight within a species is largely determined by nutritional, hormonal and environmental factors, while dress out percentages are affected by factors such as gut fill, diet and muscle (carcass) leanness (Owens et al., 1993). Carcass weight, whether measured warm or cold, is also influenced by some uncontrollable factors, such as bruising, unintentional removal of subcutaneous fat and varying levels of bleeding/dehydration during the cooling phases for example. The influence of these factors on the results is discussed where appropriate.

In Table 4, a summary of the average dead weight, carcass weight and dress out percentage of some common South African ungulate species, including the common warthog and European wild boar (*Sus scrofa*), and are given. The tabulated values are for mature (adult) animals of both sexes. The general carcass yield of the common warthogs found in this study is similar to results obtained from the study by Hoffman & Sales (2007), and overall similar to other wild ungulates (56-66%, Hoffman 2007). It is important to remember when comparing carcass yields to indicate the technical dressing methodology applied. As noted by Hoffman & Sales (2007), the dressed carcass of warthogs normally excludes the head, trotters and skin (with most of the adjoining subcutaneous fat), while the head was included in the carcass weight of the wild boars (Skewes et al., 2008). The head, skin and trotters contributed an average of 21.3% to the total dead weight for adult warthogs. If these are included in the carcass and dressed weights, and dress out percentages for warthogs (Table 2 & Table 3), they are similar to those for domestic pigs ready for slaughter (± 90kg dead weight, 70 kg carcass weight, 77.8% dress out %) (Pieterse et al., 2009).

The removal of the skin of warthogs complicates the extent to which subcutaneous fat is removed, and could have varying effects on the weight of the skin or the final carcass weight and dressing percentage. Although it is common belief that warthogs do not have subcutaneous fat (see for example Wikipedia http://en.wikipedia.org/wiki/Warthog), it was noticeable that the warthogs of this investigation had variable levels of subcutaneous fat. This was particularly noted in warthog sows during spring and in boars during autumn. What was also noteworthy was the fact that late lactating sows (only sows found with piglets of weaning age were culled) was found to have no subcutaneous fat. Due to the difficulty of separating the skin and subcutaneous fat, it was impractical to attempt to measure the fat depth/thickness as is done for domestic swine. None the less, none of the warthogs had an estimated fat depth thicker than 3 mm on the rump/rib area.

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Table 8. Dead weight, carcass weight and dress out percentage of warthog, wild boar and some common game species.

Species	Sample size	Dead weight (kg)	Carcass weight (kg)	Dress out (%)
[a]Common warthog (*Phacochoerus africanus*)	5	62.0	32.0	52.0
[b]Wild boar (*Sus scrofa*)	21	47.2	30..9	65.5
[c]Springbok (*Antidorcas marsupialis*)	8	30.4	17.4	63.8
[c]Impala (*Aepyceros melampus*)	8	41.5	23.3	58
[c]Blesbok (*Damaliscus pygargus philipsi*)	8	73.4	38.8	52.9
[d]Kudu (*Tragelaphus strepsiceros*)	18	236.3	133.9	56.5
[e]Red hartebeest (*Alcelaphus buselaphus*)	29	129.8	67.9	51.9

[a]Hoffman & Sales, 2007.
[b]Skewes et al., 2008.
[c]Van Zyl & Ferreira, 2004.
[d]Huntley, 1971.
[e]Hoffman et al., 2010.

4.2 Season

Several studies have investigated the influence of season on carcass yields and dress out percentages of native ungulate species in South Africa (Taylor et al., 2005, Hoffman et al., 2009a,b, Neethling 2012), while none have investigated the phenomenon in warthogs. Variable climatic conditions may directly affect ungulate growth, development, fecundity and demographic trends (Post & Stenseth 1999), but the influence might be more moderate in temperate regions such as South Africa. Where seasonal differences in ungulate carcass yields have been reported it was largely attributed to the effect of weather and reproductive season on a) gut fill and b) fat deposition (Taylor et al., 2005, Marshal et al., 2012). Season did not have a significant influence on the overall body weight and dress out percentage of warthogs, but dress out percentages did differ when the head, skin and feet were included as total carcass weights. This was expected as skin and trotter percentages were significantly different among seasons.

The three seasons had marked temperature and rainfall variations (Figure 1 & Figure 2) that directly influences habitat quality and resource availability, and in turn the measures of warthog body condition and weight. Increased fat deposition follows an increase in the plane of nutrition and/or the age of the animal. During dressing, the skin was removed and this caused varying levels of subcutaneous fat to also be removed. As season (and subsequent climatic conditions and resource availability) has an effect on the levels of subcutaneous fat deposition (Taylor et al., 2005, Marshal et al., 2012), it could explain the differences in total skin and dress out percentages of warthogs.

Season also had a significant effect on the percentage intestinal weight (as % of body weight) of the warthogs, with total intestinal weight being the heaviest during spring. Although classified as herbivores, warthogs are generally omnivorous and utilize almost any available food source, possibly compensating for the seasonal variation in fodder quality (Cuevas et al., 2013). Stomach and intestine weights are affected on a short term basis concerning the amount and type of food and water consumed and excreted at the time point of harvest. The quantity and quality of available forage among seasons will therefore also determine gut fill and subsequent dress out percentage of warthogs. It can be postulated that the rainy season together with the start of the farrowing season result in warthogs consuming larger quantities of green fodder high in moisture, resulting in overall heavier gut fills during spring. Nyafu (2009) found warthogs to consume a larger proportion C4 grasses during spring than during winter in the Eastern Cape. C4 grasses contain high amounts of roughage which also contributes to heavier gut fill (Gill et al., 1976).

In addition to natural grazing, the prevalence of agricultural activities in the area where crops, fodder and pastures are cultivated commercially might provide year-round food for warthogs, while livestock and game farms offer permanent water sources in the form of dams and troughs. In this specific investigation, it was noted that some of the warthogs culled during autumn and winter were found consuming corn. This was also found when examining their gut contents and it would be interesting to see whether the fatty acid profile of these animals differed from that of the animals consuming mainly grasses as it is well known that the lipid content and fatty acid profile of monogastric animals is strongly influenced by diet (Wood et al., 2008).

4.3 Sex

Male warthogs had significantly heavier carcass weights and higher dress out percentages. Other African ungulates had similar results, black wildebeest (Hoffman et al., 2009a), greater kudu, impala, (Hoffman et al., 2009b), springbok (Van Zyl & Ferreira 2004) and red hartebeest males were all heavier (Hoffman et al., 2010). Warthogs display a marked level of sexual dimorphism, and sexually dimorph ungulate males generally have larger bodies resulting in heavier dead and carcass weights. According to literature, adult male warthogs may on average weigh anything between 60-105 kg and female warthogs 45-70 kg, where adults are classified as two years and older (Estes, 1995, Stuart & Stuart, 2008). In this investigation, boars ranged from 31.5 kg to 91.6 kg and sows 37.6 to 71.1 kg.

Sexually dimorphic ungulates males usually also have additional extremities such as horns and/or tusks which could affect the overall dress out percentage. Warthogs do not have horns but both sexes have tusks. The heads from the male animals were significantly heavier than the females, and although tusk weight was not measured in this study, it could partly explain the heavier head weight of males. No research has been conducted on differences in tusk size but males do utilize their tusks during fighting and may be genetically pre-disposed to larger tusks. While this might contribute to larger tusks and heavier average head weight, the removal of the head should result in a lower dress out percentage. Male dress out percentage was still significantly higher than for females. However, when including the head, skin and trotter weights to calculate the carcass weight and dress out percentages, the adjusted carcass weights were still different between sexes, but not the adjusted dress out percentages. This could possibly be compensated for by the heavier average skin weight of females (regarding the kidneys it is argued that this difference is of no biological significance). Females might be biologically inclined to deposit increased levels of fat for reproduction, with extra subcutaneous fat unfortunately removed with the skin during dressing. This would require further investigation as to how it might affect carcass weights and dressing percentages, and also overall meat quality, for females among seasons.

5 Management suggestions

Control strategies applied to warthog populations may vary depending on the management goals. Large scale culling of animals aims to drastically reduce population numbers, while not necessarily utilizing the animals, while harvesting aims to hunt animals for meat production for the commercial market. Culling has no bias towards age or sex, while harvesting and recreational hunting is more focused on the offtake of certain groups or individuals – particularly the trophy hunting industry focuses on adult males. Sustainable utilization of warthog populations would entail regulated harvesting or hunting events that focus on the offtake of animals to decrease population numbers and acquire financial gain. Planning the aims of the proposed offtake strategy would have to take into account factors such as age, sex and season, as they are important parameters determining carcass yield and dress out percentage.

Depending on management goals, offtake strategies can be tweaked to optimize population control activities or production yields. Culling sows before the mating season (autumn) and boars after could be used as a strategy to reduce reproductive opportunities. Considering ethical hunting practices it would not be advisable to hunt sows with dependent offspring, although culling independent yearlings might reduce the number of warthogs becoming sexually active. While adult boars could provide heavier carcasses and higher dress out percentages, the effect of gender on meat quality would be important when applied to meat-culling-operations. The influence of age also still warrants investigation as it could have significant effects on carcass yield, dress out percentages and meat quality.

6 Conclusion

To summarize, this is the first study to investigate seasonal and sex effects on common warthog carcass yield and dress out percentage in South Africa. Although the sample size was small, it provides a good basis for future research. As the area under investigation does not form part of the warthog's historical natural distribution range, the results may vary according to region. It would be useful to investigate the influence of region, and therefore diet and genetics, on carcass composition and yield. The results from this investigation however show that favourable carcass yields and dress out percentages mean warthogs can be harvested and utilized for the commercial market, thereby providing farmers with an incentive to manage them in a sustainable manner. Warthog utilization can also contribute towards food security in the country.

If the meat is destined for the commercial market, the physical and chemical quality parameters of warthog meat as influenced by external factors should be investigated. Inferring from this study, season, age and sex should invariably affect the physical and chemical characteristics of the meat, and investigating these factors would provide a more comprehensive profile on the meat for consumers. As with carcass yields and dressing percentages, the harvesting and processing of warthog meat can be optimized following the guidelines obtained from such an investigation, encouraging commercial utilization and acceptance.

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8 References

Benson, D. E. (1991). Values and management of wildlife and recreation on private land in South Africa. *Wildlife Society Bulletin*, *19*, 497–510.

Carroll, T. 2010. Hunting statistics (2009). Presented at the Annual General Meeting of the Professional Hunting Association South Africa (PHASA), Fourways, South Africa, 16 November 2010. http://www.phasa.co.za/downloads/itemlist/category/18-hunting-information.html (accessed 3 March 2014).

Carruthers, J. (2008). " Wilding the farm or farming the wild "? The evolution of scientific game ranching in South Africa from the 1960s to the present. *Transactions of the Royal Society of South Africa*, *63*, 160–181.

Child, G., Roth, H. H. & Kerr, M. (1968). Reproduction and recruitment patterns in warthog *(Phacochoerus aethiopicus)* populations. *Mammalia, 32*, 6–29.

Clewer, A. G. & Scarisbrick, D. H. (2001). Practical statistics and experimental design for plant and crop science. Chichester, England: John Wiley & Sons.

Cloete, P. C., Taljaard, P. R., & Grové, B. (2007). A comparative economic case study of switching from cattle farming to game ranching in the Northern Cape Province. *South African Journal of Wildlife Research*, *37*, 71–78. doi:10.3957/0379-4369-37.1.71

Cowling, R. M., Richardson, D. M. & Pierce, S. M. (1997). Vegetation of southern Africa (pp. 224-225). Cape Town, South Africa: Cambridge University Press.

Crawford, M. A., Gale, M. M., & Woodford, M. H. (1970). Muscle and adipose tissue lipids of warthog, Phacochoerus aethiopicus. *International Journal of Biochemistry*, *1*, 654–658. doi:10.1016/0020-711x(70)90039-x

Cuevas, M. F., Ojeda, R. A., Dacar, M. A., & Jaksic, F. M. (2013). Seasonal variation in feeding habits and diet selection by wild boars in a semi-arid environment of Argentina. *Acta Theriologica*, *58*, 63–72. doi:10.1007/s13364-012-0105-x

Cumming, D. H. M. (1975). A field study of the ecology and behaviour of warthog. Museum Memoirs, 7. Salisbury, Zimbabwe: Trustees of the National Museums and Monuments of Rhodesia

DAFF (Department of Agriculture, Fisheries and Forestry). (2012). Game scheme final draft for public comments. Retrieved from http://www.nda.agric.za/vetweb/Legislation/Meatsafety/Comment/GAMESCHEMEFINALDRAFTFORPUBLICCOMMENTSonwebsite.pdf

DAFF (Department of Agriculture, Fisheries and Forestry). (2013). Abstract of Agricultural Statistics 2013. Retrieved from www.nda.agric.za/docs/statsinfo/Abstract2013.xlsx

Department of Agricultural Development.

Dry, G. (2012). Die gesig van groen. Wildlife Ranching South Africa (WRSA), (pp. 15–19). Retrieved from http://www.wrsa.co.za/wrsa-e-magazine/book/3-spring-2012-publication/2-wrsa-publications

Estes, R. D. (1995). The behaviour guide to African mammals: including hoofed mammals, carnivores, primates. Halfway House, South Africa: Russel Friedman Books.

Gill, D. R., Martin, J. R. & Lake, R. (1976). High, medium and low corn silage diets with and without monensin for feedlot steers. *Journal of Animal Science, 43*, 363–368.

Grubb, P., & D'Huart, J. (2010). Rediscovery of the Cape warthog *Phacochoerus aethiopicus*: a review. *Journal of East African Natural History*, *99*, 77–102. Retrieved from http://www.bioone.org/doi/abs/10.2982/028.099.0204

Hoffman, L. C. (2000). The yield and carcass chemical composition of impala (*Aepyceros melampus*), a southern African antelope species. *Journal of the Science of Food and Ariculture*, *80*, 752–756.

Hoffman, L. C. (2007). Inaugural address: The meat we eat: are you game? Retrieved from http://hdl.handle.net/10019.1/292.

Hoffman, L. C., & Cawthorn, D.-M. (2012). What is the role and contribution of meat from wildlife in providing high quality protein for consumption? *Animal Frontiers*, *2*, 40–53. doi:10.2527/af.2012-0061

Hoffman, L. C., & Sales, J. (2007). Physical and chemical quality characteristics of warthog meat. *Livestock Research for Rural Development*, *19*(Article #153). Retrieved from http://www.lrrd.org/lrrd19/10/hoff19153.htm

Hoffman, L. C., Crafford, K., Muller, N., & Schutte, D. W. (2003). Perceptions and consumption of game by a group of tourists visiting South Africa. *South African Journal of Wildlife Research*, *33*, 125–130.

Hoffman, L. C., Kritzinger, B., & Ferreira, A. V. (2005a). The effects of region and gender on the fatty acid, amino acid, mineral, myoglobin and collagen contents of impala (*Aepyceros melampus*) meat. *Meat Science*, *69*, 551–558. doi:10.1016/j.meatsci.2004.10.006

Hoffman, L. C., Kroucamp, M., & Manley, M. (2007). Meat quality characteristics of springbok (*Antidorcas marsupialis*). 2: Chemical composition of springbok meat as influenced by age, gender and production region. *Meat Science*, *76*, 762–7. doi:10.1016/j.meatsci.2007.02.018

Hoffman, L. C., Mostert, A C., Kidd, M., & Laubscher, L. L. (2009b). Meat quality of kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*): Carcass yield, physical quality and chemical composition of kudu and impala *Longissimus dorsi* muscle as affected by gender and age. *Meat Science*, *83*, 788–95. doi:10.1016/j.meatsci.2009.08.022

Hoffman, L. C., Muller, M., Schutte, D. W., Calitz, F. J., & Crafford, K. (2005b). Consumer expectations, perceptions and purchasing of South African game meat. *South African Journal of Wildlife Research*, *35*, 33–42.

Hoffman, L. C., Schalkwyk, S. Van, & Müller, N. (2009a). Effect of season and gender on the physical and chemical composition of black wildebeest (Connochaetus gnou) meat. *South African Journal of Wildlife Research*, *39*, 170–174.

Hoffman, L. C., Smit, K., & Muller, N. (2008a). Chemical characteristics of blesbok (Damaliscus dorcas phillipsi) meat. *Journal of Food Composition and Analysis*, *21*, 315–319. doi:10.1016/j.jfca.2007.12.003

Hoffman, L. C., Van Schalkwyk, S., & Muller, M. M. (2011). Quality characteristics of blue wildebeest (*Connochaetes taurinus*) meat. *South African Journal of Wildlife Research*, *41*, 210–213.

Hoffman, L. C., Van Schalkwyk, S., & Muller, N. M. (2008b). Physical and chemical properties of male and female mountain reedbuck (*Redunca fulvorufula*) meat. *South African Journal of Wildlife Research*, *38*, 11–16. doi:10.3957/0379-4369-38.1.11

Hoffman, L., Smit, K., & Muller, N. (2010). Chemical characteristics of red hartebeest (*Alcelaphus buselaphus caama*) meat. *South African Journal of Animal Science*, *40*, 221–228. Retrieved from http://www.scielo.org.za/scielo.php?pid=S0375-15892010000300008&script=sci_arttext

Huntley, B. J. (1971). Carcass composition of mature males blesbok and kudu. *South African Journal of Animal Sciences*, *1*, 125–128.

Jansen Van Rensburg, L. R. (1992). *'n Bemarkingsstrategie vir wildsvleis in die Republiek van Suid-Afrika*. PhD thesis, Potchefstroom University for Christian Higher Education, South Africa.

Luxmoore, R. (1985). Game farming in South Africa as a force in conservation. *Oryx, 19*, 225–231.

Marshal, J. P., Grange, S., & Marneweck, D. (2012). Seasonal variation in body condition of impala at Manyeleti Game Reserve, South Africa. *South African Journal of Wildlife Research, 42,* 128–137.

Mason, D. R. (1982). *Studies on the biology and ecology of the warthog Phacochoerus aethiopicus sundevalli Lönnberg, 1908 in Zululand, South Africa*. DSc thesis, University of Pretoria, South Africa.

Mason, D. R. (1984). Dentition and age determination of the Warthog *Phacochoerus aethiopicus* in Zululand, South Africa. *Koedoe*, *27*, 79–119.

Mostert, R., & Hoffman, L. C. (2007). Effect of gender on the meat quality characteristics and chemical composition of kudu (*Tragelaphus strepsiceros*), an African antelope species. *Food Chemistry*, *104*, 565–570. doi:10.1016/j.foodchem.2006.12.006

Mucina, L. & Rutherford, M. C. (Eds). (2006). *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19. Pretoria, South Africa: South African National Biodiversity Institute.

NAMC (National Agricultural Marketing Council). (2006). Annual report. Retrieved from http://www.namc.co.za/assets/pdf/NAMC%20Annual%20report.PDF.

Neethling, J. (2012). Impact of season on the composition and quality of male and female blesbok (*Damaliscus pygargus philipsii*) muscles. Unpublished MSc thesis, Stellenbosch University, Stellenbosch.

Nyafu, K. (2007). Warthog as an introduced species in the Eastern Cape. Unpublished MSc thesis, Nelson Mandela Metropolitan University, Port Elizabeth.

Onyango, C. A., Izumimoto, M., & Kutima, P. M. (1998). Comparison some physical and comparison of some physical and chemical propoerties of selected game meats. *Meat Science*, *49*, 117–125.

Owens, F. N., Dubeski, P., & Hansont, C. F. (1993). Factors that alter the growth and development of ruminants. *Journal of Animal Science*, *71*, 3138–3150.

Pieterse, E., Swarts, I. C., & Hoffman, L. C. (2009). The effect of porcine somatotropin (pST) and gender on production parameters and tissue yield of pigs slaughtered at 135 kg live weight, *39*, 286–295.

Post, E., & Stenseth, N. C. (1999). Climate variability, plant phenology, and northern ungulates. *Ecology*, *80*, 1322–1339.

Roberts, A. (1951.) Genus: *Phacochoerus*. In R. Bigalke, V. Fitzsimons & D. E. Malan (Eds.) *The mammals of South Africa* (1st ed.) (pp 267-269). South Africa: Trustees of The mammals of South Africa Book Fund.

Rutherford, M. C. & Westfall, R. H. (1994). *Biomes of Southern Africa: An objective categorization. Memoirs of the Botanical Survey of South Africa 63* (pp. 94). Pretoria, South Africa: National Botanical Institute.

Saayman, M., Van der Merwe, P. & Rossouw, R. (2011). The impact of hunting for biltong purposes on the SA economy. *Acta Commercii, 11*, 1–12.

Skewes, O., Morales, R., Mendoza, N., Smulders, F. J. M., & Paulsen, P. (2008). Carcass and meat quality traits of wild boar (*Sus scrofa* s. L.) with 2n = 36 karyotype compared to those of phenotypically similar crossbreeds (2n = 37 and 2n = 38) raised under the same farming conditions 2. Fatty acid profile and cholesterol. *Meat Science*, *80*, 1200–1204. doi:10.1016/j.meatsci.2009.04.017

Skinner, J. D. (1970). Game-ranching in Africa as a source of meat for local consumption and export. *Tropical Animal Health and Production., 2*, 151–157.

Somers, M. J. (1992). The implications of social structure for conservation and control of a warthog Phacochoerus aethiopicus population in the Andries Vosloo Kudu Reserve, Eastern Cape province. Unpublished MSc thesis, University of Pretoria, South Africa.

Somers, M. J. (1997). The sustainability of harvesting a warthog population: assessment of management options using simulation modelling. *South African Journal of Wildlife Research*, *27*, 37–43.

Somers, M. J., & Penzhorn, B. L. (1992). Reproduction in a reintroduced warthog population in the eastern Cape Province. *South African Journal of Wildlife Research*, *22*, 57–57. Retrieved from http://www.sabinet.co.za/abstracts/wild/wild_v22_n3_a1.html

Somers, M. J., Rasa, O. A. E., & Penzhorn, B. L. (1995). Group structure and social behaviour of warthogs Phacochoerus aethiopicus. *Acta Theriologica*, *40*, 257–281.

Stroleny-Ford, Y. (1990). Aspekte van wildboerdery in Suid-Afrika. Pretoria, South Africa:

Stuart, C. & Stuart, T. (2008). Veldgids to soogdiere van Suider-Afrika. Cape Town, South Africa: Random House Struik.

Talbot, L. M., Payne, W. J. A., Ledger, H. P., Verdcourt, L. D & Talbot, M. H. (1965). *The meat production potential of wild animals in Africa: a review of biological knowledge*. Technical Communication No. 16. Commonwealth Agricultural Bureaux, Fanham.

Taylor, W. A., Skinner, J. D., & Krecek, R. C. (2005). Seasonal body condition indices of mountain reedbuck (*Redunca fulvorufula*) in two areas of South African Highveld: the grassland and Karoo biomes. *South African Journal of Animal Sciences*, *35*, 19–29. doi:10.4314/sajas.v35i1.4045

Van der Merwe, P. & Saayman, M. (2005). Analysis of biltong hunting game species in South Africa. Potchefstroom, South Africa: Institute for Tourism and Leisure Studies School of Economics.

Van der Merwe, P., & Saayman, M. (2003). Determining the economic value of game farm tourism. *Koedoe*, *46*, 103–112. doi:10.4102/koedoe.v46i2.59

Van Zyl, L., & Ferreira, A. . V. (2004). Physical and chemical carcass composition of springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus dorcas phillipsi*) and impala (*Aepyceros melampus). Small Ruminent Research*, *53*, 103–109. doi:10.1016/j.smallrumres.2003.08.017

Vercammen, P. & Mason, D. R. (1993). *The Warthogs* (*Phacochoerus africanus* and *P. aethiopicus*). In W. L. R. Oliver (Ed.). Pigs, Peccaries, and Hippos: Status Survey and Conservation Action Plan (pp 75-84). Gland, Switzerland: IUCN/SSC Pigs and Peccaries Specialist Group,

Von la Chevallerie, M. (1970). Meat production from wild ungulates. *Proceedings of the South African Society for Animal Production*, *9*, 73–87.

Wood, J. D., Enser, M., Fisher, A V, Nute, G. R., Sheard, P. R., Richardson, R. I., … Whittington, F. M. (2008). Fat deposition, fatty acid composition and meat quality: A review. *Meat Science*, *78*, 343–58. doi:10.1016/j.meatsci.2007.07.019

Chapter 6

Physical and chemical characteristics of warthog (*Phacocoerus africanus*) meat as influenced by sex

Abstract

The common warthog has been introduced to parts of South Africa outside of its known range. The species is generally considered an agricultural pest and a threat to the natural environment. In response, farmers and land owners are employing a shoot on sight strategy, while other farmers are benefitting from hunting warthogs. This study aimed to investigate the influence of sex on the physical and chemical characteristics of six warthog muscles. The forequarter muscles appear more intensely red than those from the hindquarter and loin muscles (P = 0.01), while five of the six muscles from male warthogs had higher shear force values compared to female warthogs (P = 0.02). The six muscles varied in composition according to sex, while all of the muscles had a total protein content > 20% and total lipid content < 2.2%. The ratio of polyunsaturated to saturated fatty acids of the *Longissimus lumborum* muscle was < 0.45 which is the ratio recommended as beneficial for the human diet. The study also provides descriptive data on the characteristics of warthog yields and meat derived from juvenile warthog sows and boars. It is suggested that warthog meat should be marketed and labelled as whole muscle cuts and not as the typical commercial cuts used for domestic animals. In addition, the differences in the chemical profile between sexes and among muscles are considered negligible in terms of its nutrition and healthiness e.g. high protein and low fat content and a favourable PUFA:SFA ratio.

Keywords: warthog, *Phacochoerus africanus*, suid, game meat, physical, chemical, fatty acids, pale soft exudative

1 Introduction

The global trend towards healthier and sustainable living promotes the increased production and consumption of the meat from wild animals, also referred to as game meat. Game meat production is promoted as a low-input, high production alternative to traditional animal husbandry (Hoffman & Cawthorn, 2012, Kiley-Worthington, 2014). Compared to domestic livestock, most wild herbivores are more efficient at converting feed, more resistant to endemic pests and pathogens, less water-dependent and more adapted to climatic extremes (Child, Musengezi, Parent, & Child, 2012, Lindsey et al., 2013). In semi-arid rangelands, farming with wildlife or practising eco-agriculture promotes ecosystem biodiversity and health; where wild herbivores co-occur with livestock they positively contribute to grass species abundance and structure (Treydte, Baumgartner, Heitkönig, Grant, & Getz, 2013), increase landscape heterogeneity (Du Toit & Cumming, 1999, Veblen & Young, 2010) and facilitate livestock grazing (Odadi, Karachi, Abdulrazak, & Young, 2011).

Game animals are considered to have superior carcass and meat quality parameters, and generally produce a lean and healthy meat, which is high in protein, low in fat with a favourable fatty acid profile (Van Zyl & Ferreira, 2004, Hoffman, Kroucamp, & Manley, 2007a, Mostert & Hoffman, 2007, Hoffman, 2008, Hoffman, Smit, & Muller, 2008, Dannenberger, Nuernberg, Nuernberg, & Hagemann, 2013, Bartoň, Bureš, Kotrba, & Sales, 2014). The low lipid content and fatty acid composition of game meat is largely attributed to their forage diet and high levels of activity (Valencak & Gamsjäger, 2014). Formal game meat production for human consumption supports the sustainable harvesting of wild animals to promote conservation and responsible wildlife management. Game meat destined for the formal market is produced by farms and reserves that farm with or hunt wild animals, and is also a by-product of hunting for recreation, population management or problem animal control purposes. In Namibia, safari hunting accounts for the majority of game meat produced (Van Schalkwyk & Hoffman, 2010, Lindsey et al., 2013). More than 95% of the game meat produced annually (between 15 917 000 and 24 952 000 kg) is consumed within the country allowing for 87% of livestock meat produced to be exported. The majority of game meat produced in Zimbabwe (2 413 000 kg) and Kenya (556 000 kg) originated from game ranching in 1997 (TRAFFIC, 1997). During the six month hunting season, game meat contributes approximately 10% of red meat utilized per annum in South Africa, which was estimated at around 1 249 000 kg during 2011/2012 (Dry, 2010, Department of Agriculture, Forestry and Fisheries [DAFF], 2013).

Foreign and local hunters pay to hunt ungulate species for biltong production (a type of dried meat product) and trophy animals on ranches and reserves. These two activities generate the most revenue, while fresh game meat production only generates a small portion of the total income. The common warthog (*Phacochoerus africanus*) has historically been hunted and consumed by rural communities throughout its large distribution range across Africa. Currently the species also occurs extra-limitally in parts of South Africa through deliberate introductions and subsequent range expansion. Warthogs are hunted by agricultural producers for damage reprisal, and by recreational and trophy hunters (Nyafu, 2009, Swanepoel, Leslie, & Hoffman, 2016, Chapter 4). This produces a carcass of which the meat can be used for human consumption, as warthogs have a high dressing percentage, low total intramuscular lipid content, high total protein and moisture content and a favourable fatty acid profile (Hoffman & Sales, 2007, Swanepoel, Leslie, & Hoffman, 2014, Chapter 5). The general carcass yield of common warthogs and other wild ungulates average around 56-66% for mature (adult) animals of both sexes (Hoffman, 2008), similar to the 65.5% for wild boars (*Sus scrofa*) (Skewes, Morales, Mendoza, Smulders, & Paulsen, 2008). However, the dressed carcass weights of wild boars normally include the head and skin, while that of domestic pigs include the head, trotters and skin (with most of the adjoining subcutaneous fat). If the weights of the head, skin and trotters are included in the calculation of the average dress out percentages for warthogs, these percentages (75.1-78.7%) are similar to those for domestic pigs slaughtered in South Africa (74.2-79.2%) (Pieterse, 2006, Swanepoel et al., 2014, Chapter 5). While the body weight of ungulate species are inherently different, intraspecies variation in dress out percentages is influenced by gut fill, diet and muscle (carcass) leanness. Furthermore, the diet of monogastric Suidae primarily influences the lipid content and fatty acid profile of the meat (Wood et al., 2008).

Regardless of these findings, the meat from hunted warthogs is still relatively under-utilized by hunters and/or the commercial sector. Utilizing game meat would not only contribute towards food security but could also initialise a formal chain of warthog meat production for the commercial market whilst promoting sustainable wildlife utilization. The sensory and nutritional composition of game meat is determined by physical parameters of the muscle which includes the age, gender, muscle type, carcass weight and degree of fattiness (Lawrie & Ledward, 2006), while the differences in physical and chemical characteristics influence palatability and therefore consumer enjoyment and acceptance. According to Harrington (1994) and Richardson (1994), consumers regard the sensory, health related and nutritional properties the most important factors when making purchasing decisions, and the raw product should satisfy consumers' expectations regarding distinctive visual qualities with the additional benefit of being healthier and organic (Grunert & Valli, 2001, Radder & Le Roux, 2005). In addition, it has been suggested that general ignorance regarding the quality aspects of game meat, and notably preparation methods, has been the crippling factor in the growth of the fresh game meat industry. Educating consumers on the quality aspects and preparation of fresh game meat should be imperative prior to and at point of purchase.

As noted by Hoffman, Mostert, Kidd, and Laubscher (2009a), the differences in game animals in terms of species, sex and season should be considered in the light of whether they would influence meat classification and marketing. A number of studies contended that game meat should be classified and marketed according to species and rearing system (wild or farmed) considering the significant differences in fatty acid composition and associated sensory characteristics (Rødbotten, Kubberød, Lea, & Ueland, 2004, Hoffman, Mostert, & Laubscher, 2009b, Valencak, Gamsjäger, Ohrnberger, Culbert, & Ruf, 2015). In addition, the meat from wild animals has often been sold under collective terms of 'game meat' and 'venison', while it has been suggested that wild animal muscles are sold as separate units rather than the typical commercial cuts. Since meat consumption is primarily influenced by availability, price and tradition (Bender, 1992), educating producers and consumers on the quality characteristics and preparation of game meat is necessary to encourage game meat consumption. The aim of this study was to investigate the influence of sex and culling season on six different muscles of warthogs as pertaining to the physical and chemical properties.

2 Methods

2.1 Study area

Free-roaming warthogs were culled on farms in the Northern Cape and Free State provinces, around the city of Kimberley (28° 44' 31' S, 24° 46' 19' E), South Africa. Farms (N=12) over a surface area of 2 000 km^2 were identified that would possibly allow the culling of warthogs on the properties. Farmers/land-owners were contacted and the purpose of the research was explained, after which permission was asked to cull warthogs on their properties. Farmers were assured that culling would be conducted as ethically as possible, and hunters with sufficient experience would use their own registered weapons to cull the animals.

2.2 Harvesting, slaughtering and physical measurements

Although other studies used tusk protrusion and molar eruption as the basis for classifying age classes (Mason, 1984), the data capturing team had difficulty in judging their age in the field during culling as warthogs have a secretive and avoidance behaviour towards humans/vehicles, animals were shot as they were observed without any bias towards sex or age. Animals weighing less than 35 kg, with no tusk protrusion past the flanges of the lips were classified as juveniles, and all other animals classified as mature adults. A total number of 58 warthogs were shot using single shot bolt action rifles (Ethical clearance number: 11LV_HOF02). The number of warthogs culled per group regarding age and sex is depicted in Table 1. However, there were further difficulties experienced during culling events according to season, as warthogs of certain ages and sexes were observed more often during certain seasons and therefore culled accordingly (refer to Table 1) and the sampled populations varied greatly in terms of season, sex and age. While the study attempted to obtain sufficient material to allow for an investigation of the effect of sex, age and season, there were unfortunately too many imbalances in the composition of the sampled population. Therefore, only the effect of sex between adults was considered here for statistical analysis, while the data from the juvenile warthogs are provided as descriptive results.

Immediately after shooting, the animals were exsanguinated by thoracic sticking, transported to a slaughter facility and weighed and dressed according to the *Guidelines for the Harvesting of Game Meat Export* (Van Schalkwyk & Hoffman, 2010). The body weight of the animal was defined as the total weight of the animal (minus the blood lost during exsanguination), while carcass weight refers to the weight after the animal has been dressed. Dressing and evisceration entailed the removal of the head, whole thoracic and intestinal cavity's contents, feet and skin. The head was removed by making a horizontal cut between the axis and atlas bones of the neck vertebrae. The front pair of feet was removed by making a horizontal cut across the radius and ulna bones directly above the carpal joint, while the back pair was removed by cutting through the tarsal and tibia bone directly below the point where the fibula fuses with the tibia. The skin was removed by starting at the anus and working towards the neck area, while attempting to leave as much subcutaneous fat (when present) on the carcass as possible. After evisceration the carcass was washed, allowed to drip dry for ± 20 minutes before being weighed again to determine hot carcass weight. The external extremities and internal organs were weighed and stomachs were opened and visually inspected to determine whether the warthog have consumed notable quantities of maize.

After the carcass was dressed it was hanged in a cold room at 4ºC for 24 hrs before the selected muscles were excised. The six muscles chosen for analyses included the *Longissimus lumborum* (LL) (T_{12}/T_{13} to L_5), *Biceps femoris* (BF), *Semimembranosus* (SM), *Semitendinosus* (ST), *Infraspinatus* (IS) and *Supraspinatus* (SS). The muscles obtained from the right side of the carcass were used for physical analysis, while the muscles from the left side were vacuum packed, frozen at -4ºC and transported to Stellenbosch University for chemical analysis. The physical analysis took place at the slaughtering facility.

2.3 pH

A pH measurement was taken from the *Longissimus dorsi* muscle (~3rd last rib) after exsanguination using a Crison pH25 handheld portable pH meter (Lasec (Pty) Ltd, South Africa). Before each reading, the meter was calibrated with standard buffers (pH 4.0 and pH 7.0) as provided by the manufacturer. Measurements were taken at time of death, at 45 minutes later and at 2 hours post mortem and so forth until the pH stabilized. A final measurement was taken at 24 hours post mortem. The pH measurements of the individual muscles were also recorded after they were excised post-mortem and considered as ultimate pH (pH_u).

2.4 Colour

Each muscle was individually weighed before being cut perpendicularly to the longitudinal muscle fibers into 1 cm thick sections. Samples were allowed to bloom for 30 minutes and instrumental colour measurements taken in triplicate at three different positions on the cut surfaces (Stevenson, Seman, Weatherall, & Littlejohn, 1989). A Colour guide 45°/0° colorimeter (Catalogue no: 6805; BYK-Gardner, USA) was used to measure the L* (lightness), a* (red-green range) and b* (blue-yellow range) values. The hue angle (h_{ab}°) and chroma value (C*) were calculated respectively using the measured a* and b* values and the following equations (Commission International de L'Eclairage, 1976):

$$h_{ab} = \tan^{-1}\{b^*/a^*\}$$

$$C^* = \sqrt{(a^*)^2+(b^*)^2}$$

2.5 Drip loss and cooking loss

A cut section (steaks ± 1cm) of each muscle was used for the drip loss analysis as set out in the methods described by Honikel (1998). The drip loss was calculated as the percentage weight loss after samples were prepared and hung for 24 hours. The cooking loss was determined according to the methods described by Honikel (1998). Cooking loss was measured as the total weight loss after samples (steaks ± 1cm) were placed in baking bags in a water bath at 80°C for 1 hour. Before being weighed the samples were allowed to cool at 4°C and blotted dry.

2.6 Water holding capacity

A sample cut from the centre of each individual muscle was finely chopped using a scalpel and tweezers, and a 0.5 g sample was weighed out and placed on top of a filter paper (Lasec, Paper Filter, grade 292, dia.90 mm, part nr. FLAS3205090). The paper and sample was pressed between two Perspex plates for 60 sec at 588N pressure. A photo was taken of the sample after the 60 sec. Using Image J Software (Version, 1.36b), the ratio between the inner meat sample area and the liquid outside area was calculated as the water holding capacity for 0.5g sample.

2.7Shear force

The Warner-Bratzler shear force (WBSF) test was used to determine the instrumental shear force of the cooked meat samples as described by Honikel (1998). The cooked samples were placed in bags and refrigerated at 4°C before being subjected to analyses. Using a core borer, five 12.7 mm in diameter samples were cut from each individual piece parallel to the muscle fibre, avoiding the inclusion of visible connective tissue. A WBSF blade (Voisey, 1976) was used to determine the shear force required to cut the meat sample perpendicularly to the muscle fibres at a crosshead speed of 200 mm/min. Shear values were recorded as g/1.27cm diameter which was converted to Newton (N), and an average between the five replications was calculated.

2.8 Sample preparation for chemical analysis

All six muscles from the left side of carcass were defrosted overnight (12h) at 4°C. The visible fat and tendons were removed before the sample was homogenized, vacuum packed and frozen at -20°C. The samples were defrosted again overnight before chemical analysis was performed. All chemical analyses were performed in duplicate.

2.9 Proximate analyses

The determination of the total moisture, ash and crude protein content (%) was done according to the Association of Official Analytical Chemist's Standard Techniques (AOAC) method 934.01 (for moisture content), method 942.05 (for ash content) and the Dumas combustion method 992.15 (for crude protein content) (AOAC 1992, 2002a, 2002b, respectively). Total moisture content was determined using a 2.5 g homogenized sample. The moisture-free sample was used to determine total ash content. A 0.15 g, defatted, dried and finely ground sample was used for crude protein analysis with a Leco Nitrogen/Protein Analyser (FP – 528, Leco Corporation). Before the analyses the machine was calibrated using 0.15 g ethylenediamineteraacetic acid (EDTA) samples (Leco Corporation, 3000 Lakeview Avenue, St. Joseph, MI 49085-2396, USA, Part no.502-092, Lot no. 1055). After 20-30 analyses the machine was again calibrated with EDTA samples. The percentage Nitrogen (% N) per sample was multiplied by a conversion factor of 6.25 to calculate the total crude protein content per sample. The chloroform/methanol (1:2 vol/vol) extraction method as described by Lee, Trevino, and Chaiyawat (1996) was used to determine the total lipid content using a 5 g sample. The laboratory at the Department of Animal Sciences, Stellenbosch University, is accredited by the Agricultural Laboratory Association of South Africa (AgriLASA) to perform accurate and reliable proximate analyses and for validation of accuracy and repeatability partakes in monthly inter-laboratory blind tests.

2.10 Fatty acid analysis

The fatty acid analyses were only conducted on the LL muscles. For the fatty acid analysis, the lipids were extracted using a chloroform/methanol (1:2 v/v) solution according to Folch, Lees, and Sloane-Stanley (1957). The extraction solution contained 0.01 % butylated hydroxytolene (BHT) to act as an anti-oxidant. The 2 g meat sample and 20 ml solution was homogenized using a polytron mixer (Kinematica, type PT 10–35, Switzerland). Heptadecanoic acid (C17:0) was added (0.5 ml) to the homogenized sample as an internal standard in order to quantify the observed fatty acids in the sample (Internal standard: Catalogue number H3500, Sigma-Aldrich Inc., 3050 Spruce Street, St. Louis, MO 63103, USA). A 250 µL sub-sample of the extraction was transmethylated for 2 h at 70ºC in a water-bath using a methanol/sulphuric acid (19:1, v/v) as transmethylating agent (2 ml). The transmethylated sample was cooled to room temperature before the fatty acid methyl esters (FAME) were extracted by adding 1 ml dH_2O (distilled water) and 2 ml hexane to the sample and transferring the top hexane layer to a separate tube. This FAME sample was then dried under nitrogen, after which 50 µL hexane was added. A 1 µL of the FAME sample was injected into a Thermo Finnigan Focus gas-chromatograph (GC) (Thermo-Electron S.p.A, Rodana, Milan, Italy), equipped with a flame ionized detector and a 60 m BPX70 capillary column (internal diameter 0.25 mm, 0.25 µm film, SGE International, Ringwood, Victoria, Australia). The flow rate of the hydrogen gas carrier was 30 mL/min with the following temperature settings: initial temperature 60ºC, injector 220ºC, detector 260ºC and final temperature 160ºC. The injection volume of the GC was 1 µL with an approximate run time of 45 minutes. The FAME values were determined by comparing the FAME samples with a standard FAME mixture (Supelco, 37 Component FAME mix C4-C24, Cat, no. 47885-U. Supelco, North Harrison Rd, Bellefonte, PA 16823-0048, USA). Results were given as a percentage (%) of the total fatty acids present.

2.11 Statistical analysis

The physical and chemical data was analysed for each muscle separately by Analysis of variance (ANOVA) using SAS software (Statistical Analysis Software, Version 9.2, SAS Institute Inc., Cary, NC, USA). Due to the imbalances in the data, only the data from all the adults was subjected to statistical analysis, with sex as the main effect. Observations for the different muscles were also combined in a split-plot analysis of variance with muscle as sub-plot factor. The model for the Anova (according to the experimental design) is indicated by the following equation:

$$y_{ijk} = \mu + s_j + s(o)_{ik} + m_k + sm_{jk} + \varepsilon_{ijk}$$

The terms within the model are defined as: the response obtained for the ith observation for the jth sex (y_{ij}), the overall mean (μ), the sex main effect (s_j), the correct error term for testing the sex main plot effect ($s(o)_{ik}$), the effect of muscle type (m_k), the interaction effect (sm_{jk}) and the random error (ε_{ijk}) associated with response on the i^{th} observation in the j^{th} sex on the kth muscle. Shapiro-Wilk test was performed on the standardized residuals from the model to test for normality (Shapiro & Wilk, 1965). In cases where there was significant deviation from normality, outliers were removed when the standardized residual for an observation deviated with more than three standard deviations from the model value (Glass, Peckham, & Sanders, 1972). For post hoc testing, Fisher's LSD was used when the main effects/interactions analysed were significant. A 5% level of significance was used as a guideline to explain significantly differences. A non-linear regression was fitted to the pH data with time as the independent variable. The regression was conducted by the equation:

Y = a*exp(b*(c^X))

The terms are defined as: Y is the dependent variable (pH), X is the independent variable (time), a gives an indication of the minimum pH value obtained, b is the intercept of the line with the y-axis and c is the exponential constant. The regression plots indicate the mean and individual pH measures at each time with 95% confidence limits for the mean and individual observations respectively.

3 Results

3.1 Physical characteristics

The number of the culled warthogs included for physical and chemical analysis regarding season, sex and age is depicted in Table 1, and the average carcass yields and dress out percentages are depicted in Table 2. The adjusted carcass weight and adjusted dress out percentages for the adults warthogs were also calculated with the head, skin and trotters included (Table 2). The average carcass weight, dress out (%), and adjusted carcass weight was higher for males compared to females ($P = 0.03$, $P < 0.01$, $P = 0.02$, respectively) but not the adjusted dress out percentage ($P = 0.41$). The total contribution made by the skin ($P < 0.01$) and head ($P = 0.03$) to total body weight was also higher in males than females. The kidneys were the only organ that differed between males and females ($P < 0.01$) with the later having the lighter mean kidney weight. Testes made a 0.24% contribution to the total body weight of males. A total of eight adult female warthogs culled during the spring season were found to be pregnant, with an average litter size of 3.9 (± 0.3) piglets. The highest contribution made to total body weight by a litter was 6.08% (4 piglets with an average weight of 910g) and the lowest was 1.97% (3 piglets with an average weight of 327g). During the dressing procedure it as noted that the warthogs had varying levels of subcutaneous fat, while nine warthogs had stomachs full of maize.

Table 9: The number of warthogs culled per group regarding season, sex and age included for physical and chemical analysis.

	Autumn		Winter		Spring		
Sex	Female	Male	Female	Male	Female	Male	Total
Adult	9	3	3	13	13	6	47

	Autumn		Winter		Spring		
Sex	Female	Male	Female	Male	Female	Male	Total
Juvenile	1	4	2	0	2	2	11
Total	10	7	5	13	15	8	58

Table 10. The average (± SE) carcass yields and dress out percentages of adult male and female common warthogs.

Variable	Females (n = 25)	Males (n = 21)
Dead weight (kg)	51.95 ± 1.69	61.23 ± 4.55
Carcass weight (kg)	27.0^{b} ± 0.96	35.24^{a} ± 2.59
Dress out (%)*	52.14^{b} ± 0.91	57.16^{a} ± 0.91
Skin (%)*	7.47^{a} ± 0.33	7.18^{b} ± 0.27
Trotters (%)*	1.37 ± 0.04	1.52 ± 0.08
Head (%)*	11.99^{b} ± 0.23	12.91^{a} ± 0.31
Total intestine (%)*#	23.52 ± 0.99	22.05 ± 1.32
Heart (%)*	0.48 ± 0.02	0.52 ± 0.03
Liver (%)*	1.43 ± 0.04	1.40 ± 0.05
Lungs (%)*	0.78 ± 0.05	0.74 ± 0.06
Spleen (%)*	0.13 ± 0.01	0.15 ± 0.01
Kidneys (%)*	0.24^{b} ± 0.01	0.32^{a} ± 0.01
Stomach (%)*#	3.48 ± 0.53	3.13 ± 0.38
Adjusted carcass weight (kg)#	39.36^{b} ± 1.25	52.03^{a} ± 4.30
Adjusted dress out (%)##	75.07 ± 0.83	78.71 ± 1.18

[a,b]Means within the same row with different superscripts are significantly different ($P < 0.05$).
*Variables were calculated as a percentage of dead weight.
*#Total intestine weight and stomach weight was measured as full intestine and full stomach weight.
#Adjusted variables were calculated with head, skin and trotter weights included.
##Adjusted variables were calculated as percentage adjusted carcass weight of dead weight.

As warthogs are known to exhibit the phenomenon known as pale, soft and exudative (PSE) meat typically found when the pH_{45} is <6, the warthogs were categorised into two groups, those that could be classed as PSE ($pH_{45} < 6$) and those that could be classed as normal ($pH_{45} > 6$). In Table 3, the pH_{45} and pH_{24} of the LL muscle is presented according to the total adults with $pH_{45} < 6$ and $pH_{45} > 6$. The imbalances in the data did not allow for statistical comparison of any of the parameters evaluated between the two groups or sexes within a group. When considering the ultimate pH of the six muscles (Table 4), an interaction between sex and muscle for the pH_u was observed with the pH_u being the highest in the IS and SS muscle in both sexes ($P < 0.01$). There was no interaction between sex and muscle for any of the physical components unless where stated.

A regression of the pH decline in adult LL muscle according to time presented is presented in Figure 1, with the points of measure designated as 0 time (immediately after culling), 45 minutes, two hours, 10 hours, 12 and 24 hours after culling. A total of 11 warthogs had a $pH_{45} < 6$, of which five were adults and six were juveniles, but there were unfortunately only repeated pH measurements taken for two adult warthogs. Therefore, the non-linear regression presents the decline of pH for two of the animals with $pH_{45} < 6$, and for 17 animals with $pH_{45} > 6$ separately for the mean and individual observations (Figure 1). The equation for each group was: $pH_{45} < 6 = 5.51*\exp(0.16*(0.41^{\wedge}\text{Hour post mortem}))$ ($R^2 = 0.93$, $P < 0.01$) and $pH_{45} > 6 = 5.45*\exp(0.22*(0.64^{\wedge}\text{ Hour post mortem}))$ ($R^2 = 0.85$, $P < 0.01$).

Table 11: The mean (± SD) initial (pH_{45}) and final pH (pH_{24}) values of the *Longissimus lumborum* of adult warthogs categorised according to pH_{45} class (prior to dressing).

	pH class	
	PSE	Normal
	$pH_{45} < 6$	$pH_{45} > 6$
pH_{45}	5.56 ± 0.236	6.24 ± 0.218
pH_{24}	5.39 ± 0.049	5.43 ± 0.145
n = (F, M)	(4, 1)	(5, 12)

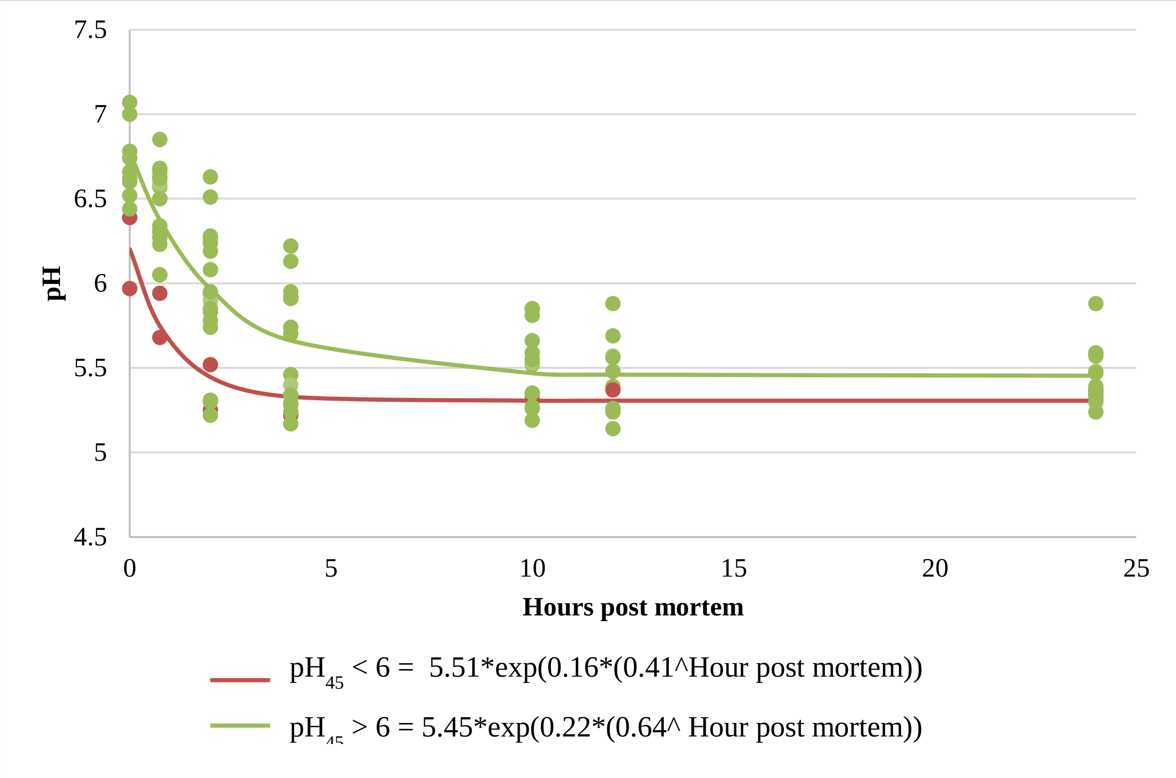

Figure 15: The decline in the pH of the *Longissimus lumborum* (LL) muscle of warthogs during the first 24 hours for warthogs with pH45 < 6 (n = 2) and warthogs with pH45 > 6 (n = 17).

The muscles from male warthogs were heavier on average compared to females ($P < 0.01$). Overall, the lightness (L*) values were lower for the IS and SS from males and females, and higher for the LL and ST from both sexes, although not all comparisons were significantly different (Table 4). The redness (average a*) values was higher for the IS and SS ($P < 0.01$), significantly so for these muscles from females compared to males ($P = 0.01$), while the LL muscle from both sexes had the lowest redness values ($P < 0.01$). The SM muscle from both sexes had the highest yellowness (b*) values ($P < 0.01$), which did not differ significantly from the male BF, while the BF and LL muscles from females had lower b* values than males ($P = 0.01$). Overall, the hue-angle values were highest for the LL muscle from both sexes, while the LL muscle from females did not differ from the ST from both sexes (Table 4).

While the chroma values were generally higher for the IS and SS muscles ($P < 0.01$), there was no difference between sexes for all six muscles. There was also no difference in cooking loss or water holding capacity (WHC) between sexes for all six muscles, while the cooking loss was lowest for the LL muscles ($P < 0.01$). The ST from females had a higher drip loss ($P < 0.01$) which did not differ from the BF from females, and lowest shear force values ($P < 0.01$), which did not differ from the female LL and male IS. Overall, the drip loss was lowest in the BF, IS and SS muscles, and the shear force values were higher for the muscles from male animals ($P = 0.02$) except for the IS muscle which had lower shear force values compared to the female IS although the difference was not significant.

Although the culling was conducted as ethically as possible with regards to animal welfare, some warthogs (adults = 5, juvenile = 6) were considered to have experienced acute ante-mortem stress as their pH_{45} was < 6 (typical of pigs indicating the PSE phenomenon). pH_{45} did not correlate with drip loss ($r = -0.27$, $P = 0.16$) of *Longissimus lumborum* muscle, but was negatively correlated with WHC ($r = -0.54$, $P < 0.01$), and average L* ($r = -0.67$, $P < 0.01$), and positively with pH_0 ($r = 0.86$, $P < 0.01$) and tenderness (shear force) ($r = 0.76$, $P < 0.01$).

Table 12: The mean (± SD) physical analysis values of the six adult warthog muscles according to sex.

		Muscle[1]					
Component	Sex	LL	BF	SM	ST	IS	SS
Mass (g)	Female	574.0^{c} ± 269.92	703.5^{bc} ± 149.05	668.9^{bc} ± 134.62	229.9^{e} ± 48.29	225.3^{f} ± 91.23	237.1^{e} ± 65.05
	Male	607.4^{bc} ± 251.27	828.7^{a} ± 335.15	805.6^{ab} ± 284.15	263.4^{e} ± 68.63	321.9^{de} ± 174.95	363.7^{d} ± 188.07
n = (F, M)	21, 15	18, 15	21, 15	21, 15	21, 15	21, 15	21, 15
pH_u	Female	5.50^{def} ± 0.140	5.52^{e} ± 0.172	5.47^{def} ± 0.141	5.50^{de} ± 0.151	5.77^{a} ± 0.195	5.69^{ab} ± 0.207
	Male	5.41^{f} ± 0.103	5.47^{ef} ± 0.103	5.48^{def} ± 0.240	5.57^{cd} ± 0.215	5.57^{c} ± 0.119	5.65^{bc} ± 0.232
n = (F, M)		21, 14	21, 15	21, 15	21, 15	21, 15	21, 15
L*	Female	44.62^{ab} ± 3.47	39.11^{e} ± 3.77	43.83^{ab} ± 4.64	45.08^{a} ± 4.46	34.79^{f} ± 3.67	35.17^{f} ± 2.98
	Male	44.65^{ab} ± 3.33	40.05^{de} ± 4.30	41.57^{cd} ± 3.37	42.89^{bc} ± 3.93	34.15^{f} ± 3.14	34.80^{f} ± 3.31
n = (F, M)		21, 15	21, 15	21, 15	21, 15	21, 15	21, 15
a*	Female	8.06^{f} ± 2.52	11.52^{c} ± 2.15	11.20^{c} ± 2.42	9.29^{d} ± 3.33	14.84^{a} ± 1.66	14.80^{a} ± 2.13
	Male	7.87^{f} ± 1.81	11.08^{c} ± 1.82	10.62^{c} ± 2.06	9.47^{d} ± 2.36	13.70^{b} ± 1.46	13.67^{b} ± 1.39
n = (F, M)		21, 15	21, 15	21, 15	21, 15	21, 15	21, 15
b*	Female	8.45^{de} ± 2.40	8.62^{cde} ± 1.17	10.47^{a} ± 2.40	9.09^{bcde} ± 1.51	8.35^{e} ± 0.99	9.07^{bcde} ± 0.78
	Male	9.24^{bcd} ± 1.83	9.86^{ab} ± 1.97	10.18^{a} ± 1.46	9.31^{bcd} ± 1.25	8.80^{cde} ± 1.21	9.11^{bcde} ± 1.82
n = (F, M)		21, 15	21, 15	21, 15	21, 15	21, 15	21, 15
Hue angle	Female	47.26^{ab} ± 7.72	37.16^{e} ± 6.60	43.12^{cd} ± 6.50	45.93^{bc} ± 8.80	29.46^{g} ± 3.31	31.81^{fg} ± 3.82
	Male	49.69^{a} ± 8.10	41.63^{d} ± 5.80	44.00^{cd} ± 4.52	45.10^{bc} ± 6.90	32.77^{f} ± 4.52	33.55^{f} ± 5.33
n = (F, M)		21, 15	21, 15	21, 15	21, 15	21, 15	21, 15
Chroma	Female	11.78^{g} ± 2.42	14.48^{d} ± 1.82	15.42^{cd} ± 2.95	13.12^{ef} ± 3.13	17.05^{b} ± 1.67	17.39^{a} ± 1.95
	Male	12.25^{fg} ± 1.91	14.91^{d} ± 2.15	14.76^{d} ± 1.91	13.36^{e} ± 2.14	16.32^{bc} ± 1.42	16.50^{ab} ± 1.66

		Muscle[1]					
Component	Sex	LL	BF	SM	ST	IS	SS
n = (F, M)		21, 15	21, 15	21, 15	21, 15	21, 15	21, 15
Cooking loss %	Female	$32.17^{e} \pm 3.60$	$34.01^{cde} \pm 2.57$	$35.34^{cd} \pm 2.79$	$38.89^{a} \pm 6.54$	$34.87^{cde} \pm 5.77$	$38.50^{ab} \pm 2.19$
	Male	$32.26^{e} \pm 2.98$	$36.20^{bcd} \pm 2.74$	$36.36^{bc} \pm 2.77$	$38.79^{a} \pm 2.54$	$33.88^{de} \pm 3.01$	$38.19^{ab} \pm 5.18$
n = (F, M)		19, 12	20, 12	18, 12	18, 12	20, 12	20, 12
Drip loss %	Female	$3.73^{a} \pm 1.58$	$2.55^{bcde} \pm 0.90$	$3.74^{a} \pm 1.86$	3.34^{ab} 1.95	$1.98^{de} \pm 0.57$	$2.39^{cde} \pm 0.74$
	Male	$3.03^{abc} \pm 2.87$	$2.22^{cd} \pm 1.55$	$3.57^{a} \pm 2.21$	2.21^{cde} 1.00	$1.58^{e} \pm 0.88$	$1.99^{de} \pm 1.28$
n = (F, M)		18, 15	20, 15	18, 13	20, 15	19, 14	20, 15
WHC	Female	8.07 ± 4.43	7.73 ± 3.56	7.15 ± 3.25	7.81 ± 3.29	7.37 ± 3.01	7.61 ± 3.69
	Male	8.25 ± 3.51	7.94 ± 4.30	7.30 ± 2.32	7.54 ± 2.37	8.16 ± 3.20	8.04 ± 2.85
n = (F, M)		21, 11	20, 21	21, 11	21, 11	21, 11	21, 12
Shear force (N)	Female	$27.31^{cd} \pm 4.04$	$29.84^{abc} \pm 5.20$	$28.47^{bc} \pm 4.90$	$25.40^{d} \pm 4.41$	$28.61^{bcd} \pm 5.03$	$28.68^{bc} \pm 5.13$
	Male	$30.26^{ab} \pm 6.55$	$30.88^{abc} \pm 6.09$	$30.81^{ab} \pm 6.86$	$32.36^{a} \pm 7.18$	$27.99^{bc} \pm 7.35$	$30.09^{abc} \pm 7.52$
n = (F, M)		21, 15	21, 15	21, 15	21, 15	20, 15	21, 15

$^{a-g}$Means with different superscripts are significantly different ($P < 0.05$) for the mean L*values between muscles and sex for each specific parameter measured.
[1]*Longissimus lumborum* (LL) (T_{12}/T_{13} to L_5), *Biceps femoris* (BF), *Semimembranosus* (SM), *Semitendinosus* (ST), *Supraspinatus* (SS) and *Infraspinatus* (IS).

3.2 Chemical characteristics

The effect of sex on the chemical composition of the muscles is presented in Table 5. There was greater variation in the chemical composition between muscles than between the same muscle from males and females. Overall the muscles had a high protein (> 20%) and low fat (> 2.2) content. The mean moisture content of the SS muscle and the mean protein content of the LL muscle from the females were lower ($P = 0.02$ and $P = 0.01$, respectively), while the mean lipid content was higher for the LL, SM and SS muscle from females compared to males ($P < 0.01$).

3.3 Fatty acid profile

The fatty acid (FA) profile of the *Longissimus lumborum* is presented in Table 6. Female LL had higher stearic (C18:0), palmitoleic (C16:1), oleic (C18:1ω9c) and arachidonic (C20:4ω6) acid content ($P < 0.01$, $P = 0.01$, $P < 0.01$, $P = 0.03$, respectively) and a higher total SFA and MUFA content ($P = 0.03$, $P < 0.01$, respectively) compared to males. However, there was no difference between the polyunsaturated to saturated fatty acid (PUFA:SFA) and omega 6 to omega 3 (ω6:ω3) ratios in the LL between sexes. The FA profile of female and male warthog LL consisted primarily of palmitic (19.57, 20.79%, respectively), stearic (17.19, 16.87%, respectively), oleic (17.62, 13.36%, respectively) and linoleic acids (22.46, 25.14%, respectively). There was no difference in the fatty acid profile of the warthogs found to have maize-filled stomachs compared to the others (statistical comparison data not shown).

Table 13: The effect of sex on the mean (± SD) chemical proximate composition of the six muscles from adult warthogs.

		Muscle[1]					
Component	Sex	LL	BF	SM	ST	IS	SS
Moisture	Female	$75.1^{de} \pm 1.21$	$75.7^{bcd} \pm 1.12$	$74.7^{e} \pm 0.92$	$75.9^{abc} \pm 1.05$	$75.6^{bcd} \pm 1.16$	$75.4^{cd} \pm 1.17$
	Male	$74.5^{e} \pm 1.11$	$75.7^{bcd} \pm 0.94$	$75.1^{de} \pm 1.17$	$76.5^{a} \pm 1.15$	$76.2^{ab} \pm 1.16$	$76.5^{a} \pm 1.15$
Protein	Female	$22.7^{bc} \pm 1.54$	$21.9^{cd} \pm 1.18$	$23.1^{b} \pm 1.00$	$21.5^{d} \pm 0.99$	$21.5^{d} \pm 1.01$	$21.8^{d} \pm 1.31$
	Male	$24.2^{a} \pm 1.21$	$22.6^{bc} \pm 1.15$	$23.3^{b} \pm 1.22$	$21.5^{d} \pm 1.30$	$21.5^{d} \pm 1.10$	$21.6^{d} \pm 1.35$
Lipid	Female	$1.7^{def} \pm 0.52$	$1.7^{def} \pm 0.31$	$1.6^{e} \pm 0.27$	$1.9^{bcd} \pm 0.66$	$2.2^{a} \pm 0.52$	$2.1^{ab} \pm 0.48$
	Male	$1.3^{g} \pm 0.28$	$1.6^{f} \pm 0.24$	$1.5^{f} \pm 0.18$	$1.7^{def} \pm 0.53$	$2.0^{abc} \pm 0.31$	$1.9^{cde} \pm 0.40$
Ash	Female	$1.2^{ab} \pm 0.17$	$1.2^{ab} \pm 0.07$	$1.2^{ab} \pm 0.05$	$1.2^{a} \pm 0.31$	$1.2^{ab} \pm 0.08$	$1.2^{ab} \pm 0.05$
	Male	$1.2^{ab} \pm 0.04$	$1.2^{ab} \pm 0.07$	$1.2^{ab} \pm 0.05$	$1.2^{ab} \pm 0.05$	$1.1^{b} \pm 0.05$	$1.2^{ab} \pm 0.07$
n = (F, M)		25, 21	21, 14	21, 15	20, 15	21, 15	21, 14

[a-g]Means with different superscripts are significantly different ($P < 0.05$) between muscles and sex each specific parameter measured.
[1]*Longissimus lumborum* (LL) (T_{12}/T_{13} to L_5), *Biceps femoris* (BF), *Semimembranosus* (SM), *Semitendinosus* (ST), *Supraspinatus* (SS) and *Infraspinatus* (IS).

Table 14: The fatty acid profile (mg·g^{-1} ± SD) of the *Longissimus lumborum* of adult female and male warthogs.

Fatty acid	Common name	Female (n = 15)	Male (n = 16)
Saturated fatty acids			
C14:0	Myristic acid	0.04 ± 0.004	0.03 ± 0.004
C15:0	Pentadecanoic acid	0.03 ± 0.002	0.03 ± 0.002
C16:0	Palmitic acid	3.12 ± 0.22	2.61 ± 0.21
C18:0	Stearic acid	2.74^{a} ± 0.14	2.12^{b} ± 0.14
C20:0	Arachidic acid	0.04 ± 0.01	0.05 ± 0.01
C21:0	Heneicosanoic acid	0.02 ± 0.002	0.02 ± 0.002
C22:0	Behenic acid	0.11 ± 0.01	0.10 ± 0.12
C23:0	Tricosanoic acid	0.34 ± 0.003	0.03 ± 0.003
C24:0	Lignoceric acid	0.30 ± 0.03	0.29 ± 0.03
Monounsaturated fatty acids			
C16:1	Palmitoleic acid	0.16^{a} ± 0.02	0.08^{b} ± 0.02
C18:1ω9c	Oleic acid	2.81^{a} ± 0.28	1.68^{b} ± 0.27
C18:1ω9t	Linolelaidic acid	0.03 ± 0.002	0.02 ± 0.002
C20:1	Eicosenoic acid	0.56 ± 0.08	0.36 ± 0.07
C22:1ω9c	Erucic acid	1.16 ± 0.08	0.90 ± 0.08
C24:1	Nervonic acid	0.03 ± 0.003	0.03 ± 0.003
Polyunsaturated fatty acids			
C18:2ω6c	Linoleic acid	3.58 ± 0.17	3.16 ± 0.17
C18:3ω6	γ Linolenic acid	0.02 ± 0.001	0.02 ± 0.001
C18:3ω3	γ α Linolenic acid	0.06 ± 0.01	0.06 ± 0.01
C20:2	Eicosadenoic acid	0.06 ± 0.004	0.05 ± 0.004
C20:3ω6	Eicosatrienoic acid	0.02 ± 0.002	0.02 ± 0.001
C20:3ω3	Eicosatrienoic acid	0.06 ± 0.01	0.05 ± 0.01
C20:4ω6	Arachidonic acid	0.39^{a} ± 0.02	0.33^{b} ± 0.02
C20:5ω3	Eicosapentaenoic acid	0.04 ± 0.01	0.04 ± 0.01
C22:5ω3	Docosapentaenoic acid	0.41 ± 0.03	0.37 ± 0.03
C22:6ω3	Docosahexaenoic acid	0.10 ± 0.01	0.11 ± 0.01
SFA		6.44^{a} ± 0.37	5.28^{b} ± 0.35
MUFA		4.75^{a} ± 0.03	3.07^{b} ± 0.32
PUFA		4.75 ± 0.22	4.22 ± 2.21
PUFA:SFA		0.76 ± 0.04	0.82 ± 0.03
ω6:ω3		6.22 ± 0.28	5.80 ± 0.27

$^{a-b}$Least square means in the same row with different superscripts are significantly different (p<0.05) for sex.
SFA, saturated fatty acids; PUFA, polyunsaturated fatty acids; ω3 PUFA, omega-3 polyunsaturated fatty acids; ω6 PUFA, omega-6 polyunsaturated fatty acids; P:S, polyunsaturated to saturated fatty acids ratio.
SFA = sum of C14:0, C15:0, C16:0, C18:0, C20:0, C21:0 and C22:0; PUFA = sum of C18:2ω6c, C18:2ω6t, C18:3ω3, C18:3ω6, C20:2, C20:3ω3, C20:3ω6, C20:4ω6, C20:5ω3, C22:2, C22:5ω3 and C22:6ω3; ω3 PUFA = sum of C18:3ω3, C20:3ω3, C20:5ω3, C22:5ω3 and C22:6ω3; ω6 PUFA = sum of C18:2ω6c, C18:3ω6, C20:3ω6 and C20:4ω6; P:S = [(sum of C18:2ω6c, C18:2ω6t, C18:3ω3, C18:3ω6, C20:2, C20:3ω3, C20:3ω6, C20:4ω6, C20:5ω3, C22:2, C22:5ω3 and C22:6ω3)/(sum of C14:0, C15:0, C16:0, C18:0, C20:0, C21:0 and C22:0)].

3.4 Descriptive data of juvenile warthogs

The juvenile group consisted of five female juveniles and seven male juveniles, and thus due to sample size limitations, no statistical comparisons were made (Table 1). Male juveniles tended to have a heavier body weight (29.5kg ± 3.0) than female juveniles (19.3kg ± 3.1), but very similar dress out percentages (48.7% ± 1.7, and 48.2% ± 4.2 respectively). The contribution of total intestinal weight to body weight was higher in female juveniles (27.5% ± 2.9) than males (24.5% ± 0.6), but the rest of the carcass composition was very similar. Testes made a 0.1% (± 0.01) contribution to total weight in males. However as a result from culling conditions and sampling there were an imbalance in the number of each muscle from the female and male juveniles available for physical and chemical analysis (muscles were damage from shot placement, contaminated during dressing, or only a obtained as single LL muscles from professional hunter). The number of samples analysed from female and male warthogs was females = 4 and males = 6 for BF, LL, SM and ST, and females = 3 and males = 6 for IS and SS, unless otherwise noted in Table.

The physical analysis values are presented in Table 7. The pH_{45} and pH_{24} of six juvenile warthogs were measured (females = 2 and males = 4) and was 5.68 ± 0.169 and 5.40 ± 0.147, for the mean pH measurements, respectively. Overall the muscle from male juveniles tended to be heavier compared to females with the IS and SS muscle from males having high pH_u. Female muscle tended to have higher average a* and chroma values. There was no discernible pattern in the moisture loss indices of the muscles between the sexes. The chemical composition of the muscles appear generally similar in terms of moisture and protein content (Table 8) while some of the juvenile male muscles (BF, SM, SS) had surprisingly high levels of fat compared to juvenile females. The most abundant fatty acids of the juvenile LL are presented in Table 9.

Table 15: The mean (± SD) physical attributes of the six muscles derived from juvenile female and male warthogs.

Physical component	Sex	Muscle[1] LL	BF	SM	ST	IS	SS
Mass (g)	Female	211.75 ± 51.55	190.25 ± 148.41	280.75 ± 87.15	94.00 ± 34.24	80.00 ± 36.06	97.33 ± 37.29
	Male	351.17 ± 162.48	338.33 ± 98.89	358.83 ± 94.24	123.33 ± 49.63	104.83 ± 37.42	121.33 ± 31.43
pH_u	Female	5.43 ± 0.15	5.50 ± 0.13	5.43 ± 0.17	5.48 ± 0.16	5.84 ± 0.13	5.81 ± 0.11
	Male	5.38 ± 0.17	5.49 ± 0.13	5.42 ± 0.15	5.50 ± 0.21	6.00 ± 0.33	6.03 ± 0.49
L*	Female	52.57 ± 3.91	45.02 ± 2.99	50.15 ± 6.33	50.65 ± 2.93	48.28 ± 3.72	40.65 ± 4.64
	Male	50.56 ± 3.89	46.65 ± 3.64	51.33 ± 5.88	52.39 ± 3.53	39.53 ± 4.15	40.67 ± 1.79
a*	Female	5.46 ± 2.59	8.97 ± 2.09	8.81 ± 2.54	7.88 ± 2.11	13.99 ± 3.40	13.07 ± 5.00
	Male	5.56 ± 1.83	7.45 ± 2.34	7.50 ± 1.42	6.72 ± 1.59	12.42 ± 4.23	11.87 ± 2.78
b*	Female	9.44 ± 2.18	9.70 ± 1.76	11.14 ± 2.17	9.70 ± 1.11	10.01 ± 0.88	10.39 ± 0.87
	Male	8.55 ± 1.49	8.72 ± 1.92	10.56 ± 1.70	9.65 ± 1.92	9.45 ± 1.55	13.07 ± 8.46
Hue-angle	Female	60.93 ± 9.15	47.39 ± 7.98	51.78 ± 12.47	51.39 ± 5.87	36.37 ± 9.52	40.16 ± 13.28
	Male[2]	57.40 ± 9.32	50.03 ± 8.44	54.62 ± 4.74	55.33 ± 4.22	38.45 ± 7.85	40.61 ± 6.65
Chroma	Female	11.01 ± 2.87	13.30 ± 2.00	14.45 ± 1.35	12.55 ± 2.03	17.35 ± 2.18	16.97 ± 3.45
	Male[2]	10.31 ± 1.73	11.56 ± 2.62	12.99 ± 1.96	11.89 ± 2.33	15.71 ± 4.03	15.12 ± 2.58
Cooking loss %	Female	34.99 ± 1.27	36.81 ± 3.76	37.28 ± 2.69	38.56 ± 2.92	32.51 ± 5.10	39.49 ± 2.08
	Male	39.23 ± 9.30	35.97 ± 4.05	37.56 ± 3.37	37.80 ± 3.05	33.47 ± 4.94	37.98 ± 3.66
Drip loss %	Female	4.30 ± 1.72	3.40 ± 1.45	4.53 ± 2.28	4.04 ± 2.48	1.94 ± 0.46	3.23 ± 0.79
	Male[3]	4.38 ± 1.57	3.18 ± 0.64	4.70 ± 2.16	4.62 ± 1.53	3.22 ± 0.97	3.13 ± 0.84

		Muscle[1]					
Physical component	Sex	LL	BF	SM	ST	IS	SS
WHC	Female	7.88 ± 5.17	8.22 ± 3.51	8.02 ± 3.94	10.09 ± 6.18	5.29 ± 2.05	5.75 ± 1.83
	Male	10.86 ± 3.00	9.20 ± 2.58	9.90 ± 3.44	9.50 ± 2.91	9.87 ± 3.51	9.30 ± 3.41
N (F, M)		4, 6	4, 6	4, 6	4, 6	3, 6	3, 6
Shear force	Female[4]	2.86 ± 0.77	2.70 ± 0.74	2.56 ± 0.25	3.18 ± 0.47	2.39 ± 0.23	3.05 ± 0.71
	Male	2.54 ± 0.52	2.67 ± 0.57	2.80 ± 0.63	2.55 ± 0.50	2.32 ± 0.48	2.53 ± 0.47
n = (F, M)		4, 6	4, 6	4, 6	3, 6	2, 6	3, 6

[1]*Longissimus lumborum* (LL) (T_{12}/T_{13} to L_5), *Biceps femoris* (BF), *Semimembranosus* (SM), *Semitendinosus* (ST), *Supraspinatus* (SS) and *Infraspinatus* (IS).
[2]Male SS chroma and hue angle samples (n = 5)
[3]Male LL and IS drip loss samples (n = 5)
[4]Female IS shear force samples (n = 2)

Table 16: The mean (± SD) chemical analysis values of the juvenile female and male warthog muscles.

Chemical component	Sex	Muscle[1] LL	BF	SM	ST	IS	SS
Moisture	Female	75.58 ± 1.34	74.91 ± 1.30	75.53 ±1.29	75.53 ± 0.61	74.73 ± 1.73	75.74 ± 1.60
	Male	75.52 ± 1.47	76.78 ± 0.74	74.66 ± 1.37	75.59 ± 1.001	76.31 ± 1.25	76.23 ± 1.83
Protein	Female	22.82 ± 1.95	23.25 ± 0.80	22.48 ± 1.38	22.68 ± 1.20	23.30 ± 0.94	22.17 ± 1.14
	Male	22.95 ± 0.76	21.44b ± 0.76	23.46[ab] ± 1.67	22.78 ± 1.18	21.32 ± 1.31	20.23[d] ± 1.99
Fat	Female	1.45 ± 0.45	1.40 ± 0.17	1.29 ± 0.14	1.64 ± 0.39	1.73 ± 0.09	1.72 ± 0.15
	Male	1.53 ± 0.40	1.73 ± 0.73	1.80 ± 0.35	1.67 ± 0.67	1.97 ± 0.19	2.25 ± 0.26
Ash	Female	1.11 ± 0.10	1.20 ± 0.03	1.17 ± 0.05	1.10 ± 1.10	1.17 ± 0.02	1.20 ± 0.10
	Male	1.24 ± 0.06	1.27 ± 0.05	1.17 ± 0.06	1.18 ± 0.10	1.18 ± 0.04	1.17 ± 0.02
n = (F, M)		4, 6	4, 6	4, 6	3, 6	2, 6	3, 6

[1]*Longissimus lumborum* (LL) (T_{12}/T_{13} to L_5), *Biceps femoris* (BF), *Semimembranosus* (SM), *Semitendinosus* (ST), *Supraspinatus* (SS) and *Infraspinatus* (IS).

Table 17: The selected fatty acid profile (mg·g^{-1} ± SD) of the *Longissimus lumborum* of juvenile female and male warthogs.

Fatty acid	Female (n = 3)	Male (n = 3)
Satyurated fatty acids		
C16:0	3.00	2.90
C18:0	2.90	2.40
Monounsaturated fatty acids		
C18:1ω9c	1.68	1.97
Polyunsaturated fatty acids		
C18:2ω6c	3.99	3.31
C20:4ω6	0.51	0.32
SFA	6.91	6.28
MUFA	3.69	3.33
PUFA	5.63	4.47
PUFA:SFA	0.84	0.63
ω6:ω3	4.52	4.92

4 Discussion

It is unfortunate that the imbalance of sampled populations across seasons did not allow for the inclusion of season and age as a factor, as it is known that animal maturity and environmental factors such as season can influence the physical and chemical characteristics of meat, especially in wild animals (Neethling, Hoffman, Britz, 2013). It is suggested that future studies include these factors for investigation, as well as the influence of region in terms of origin which may also affect meat quality characteristics (Erasmus, Muller, Van der Rijst, & Hoffman, 2016). This is considered necessary with regards to warthog meat as the species is expanding its known distribution range across South Africa (Chapter 2) and as some provinces have strict regulations in terms of hunting season.

4.1 Physical characteristics

Muscle mass is related to total number of fibres (TNF), myofibre cross section area (myoCSA) and length of myofibres. There is greater variation among species regarding the TNF than myoCSA of individual muscles, which also appears to explain muscle sizes in dimorph species (Rehfeldt, Stickland, Fiedler, & Wegner, 1999). Warthogs display a marked level of sexual dimorphism, and sexually dimorph ungulate males generally have larger bodies resulting in heavier dead and carcass weights (Swanepoel et al., 2014, Chapter 5). In this study the BF, SM, IS and SS muscles of male warthogs were larger (heavier) than those of females. The hindquarter muscles, BF and SM, comprise the largest portion of the commercially valuable leg cut. The forequarter IS and SS is less valued as it is generally used in processed products (Swanepoel, Leslie, & Hoffman, 2016, Chapter 9.). However, the commercially valuable LL muscle did not differ in weight between sexes. This muscle is typically used for biltong production, a popular South African dried meat product made from beef or game. Although not statistically analysed, it appeared as if the muscles from juvenile warthog males could be heavier than those from juveniles females. This could influence overall production parameters for juvenile warthogs.

The pH of living muscles range from 7.0 to 7.2 and decreases post mortem to reach ultimate pH (pH_u) as lactic acid accumulates due to anaerobic glycolysis. The rate of pH decline and ultimate muscle pH is affected by numerous factors including genetics, breed, sex, muscle type and muscle fibre type, ante-mortem stress and post-slaughter handling. pH is one of the most important parameters to manage for in meat production, as it affects colour, flavour, tenderness, water holding capacity and shelf life of the final product, which ultimately determines consumer acceptance and eating quality. At 24 hours post mortem the desirable pH_u of meat should range between 5.3 and 5.8, as a low pH_u retards microbial growth and imparts flavour components (Honikel, 2004). According to England, Matarneh, Scheffler, Wachet, and Gerrard (2014), a pH of 5.5 inhibits the glycolytic enzyme phosphofructokinase and post mortem glycolysis which may explain the similar ultimate pH of meat from different species.

A higher ultimate pH_u results in meat that appears dark, firm and dry (DFD) as pertaining to its meat quality. DFD meat has a high final pH due to the low concentrations of glycogen at the time of slaughter, reducing the capacity for post mortem acidification. The meat has increased water-holding capacity with a higher risk of spoilage due to an increased susceptibility for micro-organisms (Lawrie & Ledward, 2006). In pale, soft and exudative (PSE) meat, the accelerated pH decline (typically found when the $pH_{45} < 6.0$) combined with high temperatures leads to the denaturation of proteins, and the meat becomes pale in colour, soft in texture and has decreased water-holding abilities (Monin, 2004). Both phenomena are associated with the meat from animals that experienced ante-mortem stress. Animals subjected to high levels of ante-mortem stress during culling, wounded animals, or animals that have been pursued for a great distance, are subjected to stress resulting in the depletion of glycogen reserves and compromised meat quality. Although all of the warthog muscles had pH_u values that fell within the normal range, eleven of the animals (adults = 5 and juveniles = 6) had a $pH_{45} < 6$, which is considered the critical pH indicative of acute ante-mortem stress. It is therefore possible that the association of $pH_{45} < 6$ with WHC and lightness (average L*) found here for adult LL muscle suggests the meat was PSE. Hoffman and Sales (2007) noted similar PSE characteristics in warthog meat when subjected to acute ante-mortem stress. However, there was no correlation between pH_{45} and drip loss found here, and all the muscles also had favourable drip loss of < 5%, as a drip loss > 5% is generally associated with PSE pork (Van der Wal, Bolink, & Merkus, 1988). Marchiori and Felício (2003) found the LTL of domestic pigs to have a faster rate of pH decline and lower pH_u values compared to wild boar, which possibly indicates that wild boars are less susceptible to ante-mortem stress, while other authors found wild boars have lower drip loss and WHC ratios compared to domestic swine (Szmańko, Górecka, Korzeniowska, Malicki, & Eeremenko, 2007). Therefore, it could also be argued that wild animals are generally subjected to less ante-mortem stress (Kritzinger, Hoffman, & Ferreira, 2004, Hoffman & Laubscher, 2010) whilst farmed livestock species usually experience some stress during the loading, transport, lairage and stunning activities in formal abattoirs. Other studies also found pre-slaughter stress appears to have negligible effects on the meat quality parameters of reindeer (*Rangifer tarandus*) (Wiklund, Andersson, Malmfors, & Lundström, 1996), red deer (*Cervus elaphus*) (Pollard et al., 2002) and pH decline in wild boar (*Sus scrofa*) (Marchiori & Felício, 2003).

Of the two adult warthogs for which repeated pH measurements were taken and indicative of PSE meat (Figure 1), only one animal was noted as being subjected to ante-mortem stress. The data capturing team recorded that this warthog was brought down with a head shot, but upon location the animal were still conscious, and a second close-range head shot was administered. The other warthog with a $pH_{45} < 6$ was brought down and found dead upon location, and noted by the team to not have experienced ante-mortem stress. However, it was not noted whether the warthogs appeared to be aware of the hunters, and/or was part of a sounder or in close proximity to other vigilant wildlife prior and during the culling operation, which could affect their vigilance and therefore possible ante-mortem stress. In addition, it is noted that all (n = 6) of the juveniles had a $pH_{45} < 6$, which could indicate that juvenile warthogs, who typically form juvenile groups or remain with their maternal sounder upon sexual maturation (~ 18 months, Somers, 1992), are more vigilant and may therefore experience elevated levels of ante-mortem stress during culling events. It was also noted that during the culling operations, juveniles tend to stay in the close vicinity of their founder allowing more than one animal to be killed whereas adults tend to run away, the former would also result in heightened ante-mortem stress. It was expected that the drip loss % will correlated with pH_{45} but this was not found in this study. However, since pH_0 (r = 0.86, $P < 0.01$), lightness (L*, r = -0.67, $P < 0.01$), WHC (r = -0.54, $P < 0.01$) and shear force (r = 0.76, $P < 0.01$) was correlated with pH_{45}, it could suggest that the meat was pale, soft and exudative (PSE). Although it was not possible to compare the differences in pH decline between sex and age classes considering the imbalances of data, it provides further evidence that warthogs could be susceptible to ante-mortem stress and the development of PSE meat with the latter having a faster rate of decrease in pH (Figure 1).

In addition, skeletal muscles also differ in the rate of pH decline and pH_u, as the glycogen and lactate content is influenced by the composition and characteristics of muscle fibres in muscles (Mancini & Hunt, 2005). The differences found here in the mean pH_u values of the six different adult warthog skeletal muscles follow this observation (Table 4) and a similar trend is observed for the six muscles from juvenile warthogs (Table 7). The forequarter muscles, IS and SS, had higher mean pH_u values compared to the hindquarter and LL muscles. The forequarter muscles from juvenile males had pH_u > 6, which could adversely affect meat quality, and this requires further investigation since the sample size in this study was small. These muscles are mainly used by warthogs for sustained low intensity activities such as walking and kneeling and should theoretically comprise of a larger proportion of oxidative rather than glycolytic metabolic myofibres. The high pH_u values are therefore indicative of low levels of lactic acid produced post mortem from low stores of glycogen in these muscles (Choe et al., 2008). The prevalence of oxidative myofibres is further supported by the colour values of the IS and SS muscles which had high CIE a* and chroma values, meaning the meat appeared more intensely red (Table 4, 7). The lower pH_u of the BF, LL, SM, ST are also considered to indicate that these muscles constitute significantly of glycolytic myofibres and produced larger quantities of lactic acid post mortem from stored glycogen, which is also supported by the colour values of all four muscles appearing lighter and less red than IS and SS. Mammalian hindquarter muscles, and the LTL muscle, are generally responsible for fast and extreme movements such as locomotion, and stability in the case of LTL, which requires the quick energy conversion from glycolytic stores in the absence of oxygen (Hyytiäinen, Mykkänen, Hielm-Björkman, Stubbs, & McGowan, 2014, Kang et al., 2011).

Although meat colour it is not an accurate indicator of palatability, it is one of the most important factors relating to consumers' expectations and willingness to purchase (Jeremiah, Carpenter, & Smith, 1972, Brewer, Zhu, & McKeith, 2001, Girolami, Napolitano, Faraone, Di Bello, & Braghieri, 2014) . Warthog muscle colour varied according to muscle type and in some cases between sexes, with forequarter, compared to hindquarter and LL, muscles appearing darker, redder and more saturated. Game meat is typically considered a red meat due to high levels of myoglobin in wild animal muscles (Onyango, Izumimoto, & Kutima, 1998), which is contributed to elevated activity or exercise levels of wild compared to domestic animals (Daszkiewicz, Kubiak, Winarski, & Koba-Kowalczyk, 2012), while colour development is influenced by pH decline, temperature, rate of metmyoglobin reduction, rate of oxygen consumption and lipid oxidation (Mancini & Hunt, 2005, Faustman, Sun, Mancini, & Suman, 2010). Muscles comprising of more red fibres are higher in fat, myoglobin, and iron, with greater oxygen consumption rates which makes them more susceptible to discolouration and lipid oxidation (Faustman et al., 2010). The warthog forequarter muscles also had higher ultimate pH values, which is linked to darker and redder meat colour from the increased association between protein and water molecules (Abril & Campo, 2001). Conversely, lower pH values increases the release of water from denatured proteins making the muscle appear lighter and more superficially wet. The differences between sexes regarding muscle colour could also be attributed to activity and sexual dimorphism, since warthogs are seasonal breeders with warthog sows being responsible for rearing piglets while boars compete for mating opportunities, meaning that their muscle use might be influenced by their life history. For example, sows might graze more than boars to obtain nutrients and increase fat deposition, which result in the forequarter muscles being more active with higher levels of myoglobin.

The differences among moisture indices were greater between adult warthog muscles than sexes (Table 4) while it was difficult to observe a trend among the muscles from juvenile warthogs regarding moisture loss indices, but these appear to be similar to adult warthogs in general (Table 7). The ability of meat to retain water influences raw and cooked product weight, protein content, tenderness and eating quality. A number of studies have investigated the WHC, cooking loss and drip loss of game meat with different results regarding the influence of species, sex, harvesting season and hunting/culling method. The WHC, cooking and drip loss values are usually correlated with pH_u of meat (Bouton, Harris, & Shorthose, 1971), with pH_u, drip loss and WHC considered significant indicators of drip loss, or exudative meat (Kusec, Kralik, Durkin, Petricevic, & Hanzek, 2007). A positive relationship between pH_u and WHC has been found for investigated game species (Onyango et al., 1998). This was also found here for the adult warthog muscles ($r = -0.65$, $P < 0.01$). Post mortem moisture loss occurs following changes in the muscle cell and myofibrilar structure and increased protein denaturation as pH declines. It becomes greater as pH approaches the isoelectric point (≈ 5.5), and when rapid pH decline occurs at high temperatures with onset of rigor. Other than the effect of pH and temperature, there is also evidence that ionic strength and protein oxidation affects the ability of fibres and fibre bundles to hold water (Huff-Lonergan & Lonergan, 2005). The overall WHC ratios of warthog meat were favourable and comparable to other game and deer species (Daszkiewicz et al., 2009, Hoffman, Smit, & Muller, 2010a). However, other authors found wild boars have lower drip loss and WHC ratios compared to domestic swine, although it can be argued that the methodology of hunting wild boars may have been responsible for these phenomena (Marchiori & Felício, 2003, Szmańk et al., 2007).

It has been demonstrated that raw meat characteristics such as drip loss, pH_u, moisture and lipid content may affect the cooking losses of muscles (Aaslyng, Bejerholm, Ertbjerg, Bertram, & Andersen, 2003, Jeremiah, Dugan, Aalhus, & Gibson, 2003, Oillic, Lemoine, Gros, & Kondjoyan, 2011). For example, meat with low total fat contents experience higher moisture loss during cooking, since meat with a high total fat content lose more fat than moisture, with lipid structures possibly protecting muscle fibres against rapid thermal denaturation and water loss (Lawrie & Ledward, 2006). However, according to Aaslyng et al. (2003) at core temperatures of ≥ 80°C the differences in raw meat quality, muscle type and cut become negligible regarding the observed variation in cooking loss. In this case, it would help explain the lack of association between cooking loss and physical and chemical properties of warthog muscles. Oillic et al. (2011) found greater variation between the different muscle types of animals than between the same muscles of different species. One of their findings was that a muscle high in insoluble collagen content (IS) had higher cooking loss at 90°C compared to a low collagen content muscle (LTL), and suggested that collagen fibres exert increased pressure on muscle fibres to expel moisture, but they did not measure collagen content in their study and referred to values from literature. This can be attributed to the fact that collagen shrinks more than myofibres at these temperatures.

Jeremiah et al. (2003) also found the total insoluble collagen content (measured as hydroxyproline) of different beef muscles correlated positively with cooking loss. Although the collagen content of warthog muscles was not measured, the general trend among beef muscles is that collagen content is higher in the SM, BF, ST and SS and lower in the IS and LL muscles (Rhee, Wheeler, Shackelford, & Koohmaraie, 2004). It is tempting to point out that the warthog muscles generally followed this trend with regards to cooking loss, but Oillic et al. (2011) concluded that collagen content and solubility cannot alone explain cooking loss. Daszkiewicz, Janiszewski, and Wajda (2009) summarized from literature the collagen content of the LTL from pigs, cattle and red deer (*Cervus elaphus* L.) which indicated that there is great variation among breeds and species, as collagen content and structure changes with animal age, diet, and muscle hypertrophy. Few studies have attempted to elucidate on the relationship between cooking loss and muscle structure as noted by Oillic et al. (2011). Since the factors governing cooking loss in animal muscles remain poorly understood, it is suggested that more research be directed towards this aspect, as it works toward increasing consumer knowledge on meat preparation and enjoyment. This is especially important if the production and promotion of game meat is to increase.

The high initial tenderness of warthog meat agrees with other studies on venison (Daszkiewicz et al., 2012, Farouk et al., 2007, Wiklund, Dobbie, Stuart, & Littlejohn, 2010), game meat (Hoffman, Kroucamp, & Manley, 2007b, Hoffman et al., 2010) and wild boar (Sales & Kotrba, 2013). The average shear force values for all the muscles were lower compared to the general threshold for beef where tenderness is denoted to shear force values < 42.28 (N) (Destefanis, Brugiapaglia, Barge, & Dal Molin, 2008). In general, tender meat is associated with a normal rate of pH decline within the desired temperature range of 10–15°C with the onset of rigor. Low pH_u values ranging around 5.5 have been positively associated with increased tenderness compared to intermediate pH_u values ranging from 5.8-6.0 for game meat (Hoffman et al., 2007a, Wiklund et al., 2010) and beef (Lomiwes, Farouk, Wu, & Young, 2014).

Although it appears as if the meat from wild animals has a higher initial tenderness compared to beef, the mechanisms involved are even less understood for wild than domestic animals. It has been suggested that post mortem proteolysis occurs at a faster rate in the muscles from game animals from the earlier activation of calpain I and calpain II post mortem compared to beef (North, Frylinck, & Hoffman, 2015, 2016). Other than intrinsic factors (muscle fibre and collagen composition), post-mortem handling and carcass chilling e.g. rate of temperature and pH decline during the onset of rigor mortis influence also muscle tenderness (Maltin, Balcerzak, Tilley, & Delday, 2003).

According to Purslow (2005) the background toughness of meat is largely attributed to variation in the amount of perimysium rather than endomysium among different muscles. The perimysium is responsible for determining muscle fibre size which has been negatively associated with meat tenderness, as shown by Taylor, Labas, Smulders, and Wiklund (2002) for moose and reindeer meat. In general, the muscle fibre bundles are large in SM muscles and small in ST muscles. The perimysium composition of muscles can change with exercise and diet and considering that warthogs are wild animals, their seasonal behaviour and activity could be responsible for differences in perimysium content and structure among muscles, influencing meat texture and tenderness (Taylor, 2004). The muscles from male warthogs had higher shear force values than females, which were expected as myofibre coarseness is higher in mature animals and in males (Lawrie & Ledward, 2006), while the shear force values for juvenile muscles appear less pronounced between sexes. This could affect the tenderness of the meat as perceived by consumers, possibly indicating that age together with sex could influence tenderness in sexually dimorph game animals. While the collagen content in raw meat correlates well with meat toughness, the contribution of connective tissue to meat tenderness decreases as cooking temperature increases (Aaslyng et al., 2003). At internal core temperatures of ≥ 80°C collagen becomes gelatinous, resulting in a decreased toughness in muscle cuts high in connective tissue. Conversely, muscles with low connective tissue become tougher likely due to increased myofibrilar toughness from actin denaturation (Bejerholm & Aaslyng, 2004).

4.2 Chemical characteristics

Myoglobin levels, nitrogen, total fat, intramuscular fat content, fatty acid profile and enzymatic functions differ among animal muscles and species, which changes with age and maturation (Lawrie & Ledward, 2006). The differences determine preparation methods, palatability, and ultimately consumer acceptance (Jeremiah et al., 2003). The general chemical composition of game meat agrees with that denoted to lean meat, which constitutes of > 70% moisture, > 20% protein, < 3 % fat and approximately 1% ash (minerals) content (Dannenberger et al., 2013, Hoffman et al., 2007b, Hoffman et al., 2010b, Hoffman et al., 2009b). This was also found for the meat derived from adult and juvenile warthog sows and boars. Wild animals have a higher muscle to fat ratio compared to livestock animals, are less prone to deposit subcutaneous fat than intra-muscular fat, and have a more favourable fatty acid profile, with an increase in the proportion of poly-unsaturated fatty acids to saturated fatty acids. The low overall lipid content and fatty acid composition is primarily attributed to their forage diet and high levels of activity (Valencak & Gamsjäger, 2014) while the large variation in intramuscar fat (IMF) content of the wild boar *Psoas major* muscle was attributed to diet and not sex or maturity (Quaresma et al., 2011). In the meat from domestic animals the total fat content is inversely related to both total moisture and protein content i.e. with increasing fat content the content of moisture and protein decreases. However, as noted by Neethling, Britz and Hoffman (2014), the overall low fat content of game meat appears to amplify the relationship between moisture and protein content. This means that the overall moisture and lipid content increased as the protein content decreased, which was the general observation for the six different warthog muscles here.

It is suggested that a combination of muscle fibre characteristics, diet and reproductive activity (life history traits) is responsible for the differences in chemical composition between warthog sow and boar muscles. It was also noted that warthogs had varying levels of subcutaneous fat. Increased fat deposition and intramuscular content follows an increase in the plane of nutrition and/or age of the animal. It is suggested that female warthogs have increased subcutaneous and intramuscular fat deposition as they build up fat stores for reproductive purposes. Reproductive expenditures has been suggested responsible for the lower fat levels following the rut season of male impala (*Aepyceros melampus*) (Hoffman, 2000), blesbok (Kroon, Van Rensburg, & Hofmeyr, 1972), and red deer (Stevenson, Seman, & Littlejohn., 1992), and the low bodily fat indexes of mountain reedbuck (*Redunca fulvorufula*) (Taylor, Skinner, & Krecek., 2005) and common eland (*Taurotragus oryx*) (Von la Chevallerie, Erasmus, Skinner, & Van Zyl, 1971, Hoffman, Van Schalkwyk, McMillin, & Kotrba, 2015). Since juvenile boars are not known to partake in reproduction activities from competition with adult boars, this could explain why juvenile boars had high levels of IMF compared to juvenile females in some muscles (Table 8). In addition, the LL muscle is the last muscle in which fat is stored in mature animals but is the first region accessed for stored energy when required (Lawrie & Ledward, 2006), which is in agreement with the overall lower levels of IMF content observed here for the LL muscles compared to other muscles.

As meat is an important source of protein and amino acids, the total crude protein content and amino acid profile are characteristics pertaining to the nutritional quality of meat (Higgs, 2000). The average crude protein content for raw red meat is 20-25g per 100g (Keeton & Eddy, 2004). Although the protein and lipid content differed between some of the female and male muscles of adults (LL, SM and SS) (Table 5) and juveniles (Table 8), this should not be considered of major consideration for meat production as they are adhere to the nutritional profile denoted to game meat, which is associated with health benefits for consumers. The IMF is generally low in the meat of game species (Neethling, Hoffman, Muller, 2016), which primarily consists of structural lipid components, phospholipids and cholesterol, with high proportions of PUFA (Fisher et al., 2000). In monogastric animals, lipid content and fatty acid profile is primarily influenced by diet (Wood et al., 2008). Palmitic (saturated), linoleic and γ-linolenic (polyunsaturated) acids are the major FA of grasses (Dungait, Docherty, Straker, & Evershed, 2010) while linoleic and λ- linolenic (and α-linolenic [ALA]) acids are essential FA as they are obtained solely from the diet. The intake and composition of these fatty acids may therefor differ in wild herbivore muscle due to the seasonal and regional variability of grasses, but there were no differences in their composition for warthog LTL between sexes. In addition, some of the warthogs had a large quantity of maize (*Zea mays*) in their stomachs when maize was available, but there were no obvious differences found attributable to this in the fatty acid profile. The general FA profile of maize is higher in MFA and PUFA than SFA (Table 10) which consists primarily of palmitic, oleic and linoleic acids (USDA National Nutrient Database for Standard Reference, 2008**)**. Quaresma et al. (2011) found a higher total SFA and MUFA, and lower total PUFA content for feral wild boar culled on farms in Portugal, and attributed this to the abundance of acorns in autumn and winter seasons, which are high in oleic, linoleic and palmitic acids.

The most abundant fatty acids of adult and juvenile warthog LL were palmitic, stearic, oleic and linoleic acid (Table 6, 9), which are the major fatty acids found in animal meat (Enser, Hallett, Hewitt, Fursey, & Wood, 1996). In particular, the contribution of palmitic and oleic acid was lower for warthog LL compared to the range determined for cattle, lamb, pigs and poultry (25–30 %, 20-47%, respectively), but higher for linoleic acid (2–20%) (Keeton & Eddy, 2004). Hoffman and Sales (2007) also found high levels of linoleic acid (26.12%) in warthog LTL. It is known that feeding pigs a diet high in oleic acid increases the content of this FA in adipose tissue (Klingenberg, Knabe & Smith, 1995), while oleic acid is the product of desaturated stearic acid which results in higher MUFA content as the SFA content decreases from the continuing desaturation of SFA to their MUFA counterparts. The differences in the noted fatty acids between sexes is attributed to the higher fat content of female LL, which supports the suggestion that females have increased IMF content and subcutaneous fat deposition from increased grazing for reproductive activities. However, sex did not affect the PUFA:SFA and ω6:ω3 ratios of the adult (Table 6) and juvenile (Table 9) warthog LL.

A PUFA:SFA ratio of ≥ 0.45 and omega 6:omega 3 (n-6:n-3) of ≤ 4 is recommended for the meats consumed by humans (Warris, 2000) as a diet high in unsaturated FA provides health benefits. The meat from game animals generally adheres to this recommendation (Hoffman et al., 2010b, Valencak & Gamsjäger, 2014, Valencak et al., 2015) and therefore appeals to the modern day consumer whom have become increasingly aware of the health attributes of game meat (MacMillan & Phillip, 2008). The LTL from both sexes had a PUFA:SFA ratio above that of the recommended ≥ 0.45 for meat (Warris, 2000). Monogastric animals have a higher proportion of polyunsaturated fatty acids in muscle and adipose tissue as these FA pass unchanged through the gastric system to be incorporated into tissues (Jenkins, 1993). A high PUFA content has also been associated with higher contraction frequencies of wild fowl and game animal muscles, compared to domestic cattle and chicken muscles (Valencak & Gamsjäger, 2014). In addition, the meat from free ranging monogastric or ruminant animals have a higher PUFA, and ω3 in particular, content, as animals extensively feeding on grasses incorporate more ω6 and ω3 PUFA fatty acids in their muscles.

The ω6:ω3 ratio has been determined as favourable for a number of wild ungulates including kudu (*Tragelaphus strepsiceros*), impala (Hoffman et al., 2009b) red hartebeest (*Alcelaphus buselaphus caama*) (Hoffman et al., 2010b), blesbok (Neethling et al., 2014) mountain reedbuck (Hoffman, Van Schalkwyk, & Muller, 2008), and red deer (Purchas, Triumf, & Egelandsdal, 2010). The ω6:ω3 ratio of warthog LL was higher than the recommended ≤ 4 for meat. Quaresma et al. (2011) and Valencak et al. (2015) found a higher ω6:ω3 ratio in the meat of wild boar, which questions the assumed high nutritional value of this particular species. However, the fatty acid composition may vary with total carcass fat content and muscle type, which is influenced by species, genetics, diet, animal age and exercise (Wood et al., 2008, Dannenberger et al., 2013, Neethling et al., 2014), while the meat from wild boar is still leaner compared to pork with a favourable PUFA:SFA ratio. The high ω6:ω3 ratio found here for warthog LL is attributed to the high contribution of linoleic acid (22.46-24.14%).

Table 18: The fatty acid profile (g/100g) of maize (*Zea mays*).

Fatty acids	g/100g
Saturated fatty acids	0.33

Monounsaturated fatty acids	0.43
Polyunsaturated fatty acids	0.49

(Source: Nutrient Data Laboratory, ARS, USDA, National Food and Nutrient Anlaysis Program Wave 12h 2008, Beltsville MD.).

5 Conclusion

Since the study found significant differences in the yields and physical profile of adult warthog muscles between sexes, it is therefore suggested that warthog meat should be marketed and labelled as whole cuts and not as composite commercial cuts typically used for domestic animals. Although, the differences in the chemical profile between sexes and among muscles are considered negligible in terms of its nutrition and healthiness e.g. high protein and low fat content and a favourable PUFA:SFA ratio for the human diet Therefore it is not considered necessary to market the meat according to sex but there is still some research required to determine whether age could significantly influence physical and chemical composition and therefore consumer desirability and acceptance. The meat from wild boar is considered as less desirable regarding aroma and flavour characteristics, while there have been reports that the fresh meat from warthogs sometimes exhibits a flavour that is compared to boar taint. Boar taint is an undesirable odour and taste which may occur in the meat from entire male domestic pigs (*S. scrofa*), but has been associated with warthog meat from both genders and animals of different age classes.

The association with a wild or livery flavour has also been found for other game animal species from southern Africa. No research has been conducted of this particular aroma or flavour in the meat from warthogs or other wild suid species, and warrants further investigation to determine its impact on consumers' willingness to buy and consume warthog meat. Increased research efforts should aim to determine and characterize the physical, chemical and sensory parameters of the meat from wild animals in general to increase wild meat production and consumption. In addition, the use of meat in processed products could extend the value chain of game meat production especially as forequarter muscles for example are considered less desired for whole cut consumption. Promoters of game meat consumption maintain that utilizing wild animals contributes towards sustainable wildlife and habitat management and local food security, while generating an income from a widely available resource. Furthermore, future trends regarding global meat consumption will benefit from increased utilization of wild animals, especially concerning species such as warthogs with high reproduction rates and environmental resilience.

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7 References

Aaslyng, M. D., Bejerholm, C., Ertbjerg, P., Bertram, H. C., & Andersen, H. J. (2003). Cooking loss and juciness of pork in relation to raw meat quality and cooking procedure. *Food Quality and Preference*, *14*, 277–288.

Abril, M., Campo, M. M., Onec, A., Sanudo, C., Alberti, P., & Negueruela, A. I. (2001). Beef colour evolution as a function of ultimate pH. *Meat Science*, *58*, 69–78.

AOAC International (2002a) Official methods of analysis. Arlington, Virginia, USA: Association of Official Analytical Chemists Inc. Loss on drying (moisture) at 95–100°C for feeds. (17th ed.) AOAC Official Method 934.01.

AOAC International (2002b) Official methods of analysis. Arlington, Virginia, USA: Association of Official Analytical Chemists Inc. (17th ed.). Ash of Animal Feed. AOAC Official Method 942.05

AOAC Official Method 992.15 (1992). Crude protein in meat and meat products including pet foods. Combustion method. *Journal of Association of Official Analytical Chemists International*, 76, 787.

Bartoň, L., Bureš, D., Kotrba, R., & Sales, J. (2014). Comparison of meat quality between eland (*Taurotragus oryx*) and cattle (*Bos taurus*) raised under similar conditions. *Meat Science*, *96*, 346–52. doi:10.1016/j.meatsci.2013.07.016

Bejerholm, C. & Aaslyng, M. D. (2004). Cooking of meat. In W. K. Jensen, D. Carrick, & M. Dikeman, M. (Eds.), *Encyclopedia of meat sciences* (pp. 343–349). Oxford, UK: Elsevier Ltd.

Bender, A. (1992). Meat and meat products in human nutrition in developing countries. FAO and INPhO, Food and Nutrition Paper 53. Rome, Italy: Food and Agriculture Organization of the United Nations. Retrieved from http://www.fao.org/docrep/t0562e/t0562e00.HTM.

Bouton, P. E., Harris, P. V, & Shorthose, W. R. (1971). Effect of ultimate pH upon the water-holding capacity and tenderness of mutton. *Journal of Food Science*, *36*, 435–439.

Brewer, M. S., Zhu, L. G., & McKeith, F. K. (2001). Marbling effects on quality characteristics of pork loin chops: consumer purchase intent, visual and sensory characteristics. *Meat Science*, *59*, 153–163. doi:10.1016/S0309-1740(01)00065-1

Child, B. A, Musengezi, J., Parent, G. D., & Child, G. F. T. (2012). The economics and institutional economics of wildlife on private land in Africa. *Pastoralism: Research, Policy and Practice*, *2*, 18. doi:10.1186/2041-7136-2-18

Choe, J. H., Choi, Y. M., Lee, S. H., Shin, H. G., Ryu, Y. C., Hong, K. C., & Kim, B. C. (2008). The relation between glycogen, lactate content and muscle fiber type composition, and their influence on postmortem glycolytic rate and pork quality. *Meat Science*, *80*, 355–362. doi:10.1016/j.meatsci.2007.12.019

Commision International de L'Eclairage. (1976). Colometry (2nd). Vienna: CIE.

Dannenberger, D., Nuernberg, G., Nuernberg, K., & Hagemann, E. (2013). The effects of gender, age and region on macro- and micronutrient contents and fatty acid profiles in the muscles of roe deer and wild boar in Mecklenburg-Western Pomerania (Germany). *Meat Science*, *94*, 39–46. doi:10.1016/j.meatsci.2012.12.010

Daszkiewicz, T., Janiszewski, P., & Wajda, S. (2009). Quality characteristics of meat from wild red deer (*Cervus elaphus* L.) hinds and stags. *Journal of Muscle Foods*, *20*, 428–448.

Daszkiewicz, T., Kubiak, D., Winarski, R., & Koba-Kowalczyk, M. (2012). The effect of gender on the quality of roe deer (*Capreolus capreolus* L.) meat. *Small Ruminant Research*, *103*, 169–175. doi:10.1016/j.smallrumres.2011.09.044

Department of Agriculture, Forestry and Fisheries (DAFF). (2013). *South African Yearbook 2012/13: Agriculture, Forestry and Fisheries*. In A. Vermeulen (Ed.) (pp 44–82). Pretoria, South Africa: Department of Agriculture, Forestry and Fisheries. Retrieved from http://www.gcis.gov.za.

Destefanis, G., Brugiapaglia, A, Barge, M. T., & Dal Molin, E. (2008). Relationship between beef consumer tenderness perception and Warner–Bratzler shear force. *Meat Science*, *78*, 153–156. doi:10.1016/j.meatsci.2007.05.031

Dry, G. (2010). Commercial wildlife ranching's contribution to the green economy. Retrieved from http://www.sawma.co.za/images/Dry_Gert_Full_paper.pdf.

Du Toit, J., & Cumming, D. (1999). Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity & Conservation*, 1643–1661. Retrieved from http://link.springer.com/article/10.1023/A:1008959721342

Dungait, J. A., Docherty, G., Straker, V., & Evershed, R. P. (2010). Seasonal variations in bulk tissue, fatty acid and monosaccharide δ13C values of leaves from mesotrophic grassland plant communities under different grazing managements. *Phytochemistry*, *71*, 415–428. doi:10.1016/j.phytochem.2009.10.010

England, E. M., Matarneh, S. K., Scheffler, T. L., Wachet, C., & Gerrard, D. E. (2014). pH inactivation of phosphofructokinase arrests postmortem glycolysis. *Meat Science*, *9*, 850–857. doi:10.1016/j.meatsci.2014.07.019

Enser, M., Hallett, K., Hewitt, B., Fursey, G. A. J., & Wood, J. D. (1996). Fatty acid content and composition of english beef, lamb and pork at retail. *Meat Science*, *42*, 443–456. doi:10.1016/0309-1740(95)00037-2

Erasmus, S. W., Muller, M., Van der Rijst, M., & Hoffman, L. C. (2016). Stable isotope ratio analysis: A potential analytical tool for the authentication of South African lamb meat. *Food Chemistry, 192,* 997–1005. doi:10.1016/j.foodchem.2015.07.121

Farouk, M. M., Beggan, M., Hurst, S., Stuart, A., Dobbie, P. M., & Bekhit, A. E. D. (2007). Meat quality attributes of chilled venison and beef. *Journal of Food Quality*, *30*, 1023–1039.

Faustman, C., Sun, Q., Mancini, R., & Suman, S. P. (2010). Myoglobin and lipid oxidation interactions : Mechanistic bases and control. *Meat Science*, *86*, 86–94. doi:10.1016/j.meatsci.2010.04.025

Fisher, A. V, Enser, M., Richardson, R. I., Wood, J. D., Nute, G. R., Kurt, E., … Wilkinson, R. G. (2000). Fatty acid composition and eating quality of lamb types derived from four diverse breed x production systems. *Meat Science, 55,* 141–147. doi:10.1016/S0309-1740(99)00136-9

Folch, J., Lees, M., & Sloane-Stanley, G. H. (1957). A simple method for the isolation and purification of total lipids from animal tissues. *Journal of Biological Chemistry*, *226*, 495-509.

Girolami, A., Napolitano, F., Faraone, D., Di Bello, G., & Braghieri, A. (2014). Image analysis with the computer vision system and the consumer test in evaluating the appearance of Lucanian dry sausage. *Meat Science*, *96*, 610–616. doi:10.1016/j.meatsci.2013.08.006

Glass, G. V., Peckham, P. D. & Sanders, J. R. (1972). Consequences of failure to meet assumptions underlying the fixed effects analyses of variance and covariance. *Review of Educational Research, 42*, 237-288.

Grunert, K. G., & Valli, C. (2001). Designer-made meat and dairy products: Consumer-led product development. *Livestock Production Science*, *72*, 83–98. doi:10.1016/S0301-6226(01)00269-X

Harrington, G. (1994). Consumer demands: Major problems facing industry in a consumer-driven society. *Meat Science*, *36*, 5–18. doi:10.1016/0309-1740(94)90029-9

Higgs, J. D. (2000). The changing nature of red meat: 20 years of improving nutritional quality. *Trends in Food Science and Technology*, *11*, 85–95. doi:10.1016/S0924-2244(00)00055-8

Hoffman, L. C. (2000). The yield and carcass chemical composition of impala (*Aepyceros melampus*), a southern African antelope species. *Journal of the Science of Food and Agriculture*, *80*, 752–756.

Hoffman, L. C. (2008). The yield and nutritional value of meat from African ungulates, camelidae , rodents, ratites and reptiles. *Meat Science*, *80*, 94–100. doi:10.1016/j.meatsci.2008.05.018

Hoffman, L. C., & Laubscher, L. L. (2010). A comparison between the effects of day and night cropping on gemsbok (*Oryx gazella*) meat quality. *Meat Science, 85,* 356–362. doi:10.1016/j.meatsci.2010.02.003

Hoffman, L. C., & Sales, J. (2007). Physical and chemical quality characteristics of warthog meat. *Livestock Research for Rural Development*, *19*. Retrieved from http://www.lrrd.org/lrrd19/10/hoff19153.htm

Hoffman, L. C., & Van Schalkwyk, S. (2011). Quality characteristics of blue wildebeest (*Connochaetes taurinus*) meat. *South African Journal of Wildlife Research*, *41*, 210–213.

Hoffman, L. C., Kroucamp, M., & Manley, M. (2007a). Meat quality characteristics of springbok (*Antidorcas marsupialis*). 1: Physical meat attributes as influenced by age, gender and production region. *Meat Science*, *76*, 755–761. doi:10.1016/j.meatsci.2007.02.017

Hoffman, L. C., Kroucamp, M., & Manley, M. (2007b). Meat quality characteristics of springbok (*Antidorcas marsupialis*). 2: Chemical composition of springbok meat as influenced by age, gender and production region. *Meat Science*, *76*, 762–767. doi:10.1016/j.meatsci.2007.02.018

Hoffman, L. C., Mostert, A. C., & Laubscher, L. L. (2009b). Meat quality of kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*): The effect of gender and age on the fatty acid profile, cholesterol content and sensory characteristics of kudu and impala meat. *Meat Science*, *83*, 737–743. doi:10.1016/j.meatsci.2009.08.026

Hoffman, L. C., Mostert, A. C., Kidd, M., & Laubscher, L. L. (2009a). Meat quality of kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*): Carcass yield, physical quality and chemical composition of kudu and impala *Longissimus dorsi* muscle as affected by gender and age. *Meat Science*, *83*, 788–95. doi:10.1016/j.meatsci.2009.08.022

Hoffman, L. C., Smit, K., & Muller, M. M. (2008). Chemical characteristics of blesbok (*Damaliscus dorcas phillipsi*) meat. *Journal of Food Composition and Analysis*, *21*, 315–319. doi:10.1016/j.jfca.2007.12.003

Hoffman, L. C., Smit, K., & Muller, M. M. (2010a). Physical and sensory characteristics of blesbok (*Damaliscus dorcas phillipsi*) meat. *South African Journal of Wildlife Research*, *40*, 158–162.

Hoffman, L. C., Smit, K., & Muller, M. M. (2010b). Chemical characteristics of red hartebeest (*Alcelaphus buselaphus caama*) meat. *South African Journal of Animal Science*, *40*, 221–228. Retrieved from http://www.scielo.org.za/scielo.php?pid=S0375-15892010000300008&script=sci_arttext

Hoffman, L. C., Van Schalkwyk, D. L., McMillin, K. W., & Kotrba, R. (2015). Intramuscular fat characteristics of Namibian common eland (*Tragelaphus oryx*). *African Journal of Wildlife Research*, *45*, 312–320.

Hoffman, L. C., Van Schalkwyk, S., & Muller, M. M. (2008). Physical and chemical properties of male and female mountain reedbuck (*Redunca fulvorufula*) meat. *South African Journal of Wildlife Research*, *38*, 11–16. doi:10.3957/0379-4369-38.1.11

Hoffman, L. C., Van Schalkwyk, S., & Müller, M. M. (2009c). Effect of season and gender on the physical and chemical composition of black wildebeest (*Connochaetus gnou*) meat. *South African Journal of Wildlife Research*, *39*, 170–174.

Honikel, K. O. (1998). Reference methods for the assessment of physical characteristics of meat. *Meat Science*, *49*, 447–457. doi:10.1016/S0309-1740(98)00034-5

Honikel, K. O. (2004). Conversion of muscle to meat: Glycolysis. In W. K. Jensen, D. Carrick, & M. Dikeman. (Eds.), *Encyclopedia of Meat Sciences* (pp. 314–318). Oxford, UK: Elsevier Ltd.

Huff-Lonergan, E., & Lonergan, S. M. (2005). Mechanisms of water-holding capacity of meat: The role of postmortem biochemical and structural changes. *Meat Science*, *71*, 194–204. doi:10.1016/j.meatsci.2005.04.022

Hyytiäinen, H. K., Mykkänen, A. K., Hielm-Björkman, A. K., Stubbs, N. C., & McGowan, C. M. (2014). Muscle fibre type distribution of the thoracolumbar and hindlimb regions of horses: relating fibre type and functional role. *Acta Veterinaria Scandinavica*, *56*, 8. doi:10.1186/1751-0147-56-8

Jenkins, T. C. (1993). Lipid metabolism in the rumen. *Journal of Dairy Science*, *76*, 3851–3863. doi:10.1016/0079-6832(78)90004-6

Jeremiah, L. E., Carpenter, Z. L., & Smith, G. C. (1972). Beef colour as related to consumer acceptance and palatibility. *Journal of Food Science*, *37*, 476–479.

Jeremiah, L. E., Dugan, M. E. R., Aalhus, J. L., & Gibson, L. L. (2003). Assessment of the chemical and cooking properties of the major beef muscles and muscle groups. *Meat Science*, *65*, 985–992. doi:10.1016/S0309-1740(02)00308-X

Kang, Y. K., Choi, Y. M., Lee, S. H., Choe, J. H., Hong, K. C., & Kim, B. C. (2011). Effects of myosin heavy chain isoforms on meat quality, fatty acid composition, and sensory evaluation in Berkshire pigs. *Meat Science*, *89*, 384–389. doi:10.1016/j.meatsci.2011.04.019

Keeton, J. T. & Eddy, S. (2004). Chemical and physical characteristics of meat/Chemical composition. In W. K. Jensen, D. Carrick, & M. Dikeman, M. (Eds.) *Encyclopedia of Meat Sciences* (pp. 210–218). Oxford, UK: Elsevier Ltd.

Kiley-Worthington, M. (2014). Ecological agriculture . Integrating low input , high productive farming with wildlife conservation. Results from the experimental farm La Combe, Drome France. *Open Journal of Ecology*, *4*, 744–763.

Klingenberg, I. L., Knabe, D. A, & Smith, S. B. (1995). Lipid metabolism in pigs fed beef tallow or high-oleic acid sunflower oil. *Comparative Biochemistry and Physiology. Part B, Biochemistry & Molecular Biology*, *110*, 183–92. doi:10.1016/0305-0491(94)00116-C

Kritzinger, B., Hoffman, L. C., & Ferreira, A. V. (2004). A comparison between the effects of two cropping methods on the meat quality of impala (*Aepyceros melampus*). *South African Journal of Animal*, *33*, 233–241. Retrieved from http://www.ajol.info/index.php/sajas/article/view/3779

Kroon, F. E., Van Rensburg, W. J. J., & Hofmeyr, H. S. (1972). Seisoenale veranderinge in chemiese samestelling van volwasse blesbokramme (*Damaliscus dorcas phillipsi*) van die Van Riebeeck Natuurreservaat. *Suid-Afrikaanse Tydskrif Vir Veekunde*, *2*, 41–44.

Kusec, G., Kralik, G., Durkin, I., Petricevic, A., & Hanzek, D. (2007). Factors discriminating between pork quality conditions. *Poljoprivreda / Agriculture*, *13*, 66–69.

Lawrie, R. A., & Ledward, D. A. (2006). *Lawrie's meat science* (7th ed.). Cambridge, England: Woodhead Publishing.

Lee, C. M., Trevino, B., & Chaiyawat, M. (1996). A simple and rapid solvent extraction method for determining total lipids in fish tissue. *Journal of AOAC International, 79*, 487–492.

Lindsey, P. A., Havemann, C. P., Lines, R. M., Price, A., Retief, T. A., Rhebergen, T., … Romañach, S. S. (2013). Benefits of wildlife-based land uses on private lands in Namibia and limitations affecting their development. *Oryx*, *47*, 41–53. doi:10.1017/S0030605311001049

Lomiwes, D., Farouk, M. M., Wu, G., & Young, O. A. (2014). The development of meat tenderness is likely to be compartmentalised by ultimate pH. *Meat Science*, *96*, 646–51. doi:10.1016/j.meatsci.2013.08.022

MacMillan, D. C., & Phillip, S. (2008). Consumptive and non-consumptive values of wild mammals in Britain. *Mammal Review*, *38*, 189–204. doi:10.1111/j.1365-2907.2008.00124.x

Maltin, C., Balcerzak, D., Tilley, R., & Delday, M. (2003). Determinants of meat quality: tenderness. *Proceedings of the Nutrition Society*, *62*, 337–347. doi:10.1079/PNS2003248

Mancini, R. A., & Hunt, M. C. (2005). Current research in meat color. *Meat Science*, *71*, 100–121. doi:10.1016/j.meatsci.2005.03.003

Marchiori, A. F., & Felício, P. E. (2003). Quality of wild boar meat and commercial pork. *Scientia Agricola*, *60*, 1–5.

Mason, D. R. (1984). Dentition and age determination of the Warthog *Phacochoerus aethiopicus* in Zululand, South Africa. *Koedoe*, *27*, 79–119.

Monin, G. (2004). Conversion of muscle to meat: Colour and texture deviations. In W. K. Jensen, D. Carrick, & M. Dikeman (Eds.), *Encyclopedia of Meat Sciences* (pp 323–330). Oxford, UK: Elsevier Ltd.

Mostert, R., & Hoffman, L. C. (2007). Effect of gender on the meat quality characteristics and chemical composition of kudu (*Tragelaphus strepsiceros*), an African antelope species. *Food Chemistry*, *104*, 565–570. doi:10.1016/j.foodchem.2006.12.006

Neethling, J., Britz, T. J., & Hoffman, L. C. (2014). Impact of season on the fatty acid profiles of male and female blesbok (*Damaliscus pygargus phillipsi*) muscles. *Meat Science*, *98*, 599–606. doi:10.1016/j.meatsci.2014.06.030

Neethling, J., Hoffman, L. C., & Britz, T. J. (2013). Impact of season on the chemical composition of male and female blesbok (*Damaliscus pygargus phillipsi*) muscles. *Journal of the Science of Food and Agriculture*, *94*, 424–431. doi:10.1002/jsfa.6281

Neethling, J., Hoffman, L. C., & Muller, M. M. (2016). Factors influencing the flavour of game meat: A review. *Meat Science*, *113*, 139–153.

North, M. K., Frylinck, L., & Hoffman, L. C. (2015). The physical and biochemical changes in springbok (*Antidorcas marsupialis*) *Longissimus thoracis et lumborum* and *Biceps femoris* muscle during ageing. *Meat Science*, *110*, 145–152. doi:10.1016/j.meatsci.2015.07.009

North, M. K., Frylinck, L., & Hoffman, L. C. (2016). The changes in springbok (*Antidorcas marsupialis*) *Longissimus thoracis et lumborum* and *Biceps femoris* muscle during the rigour period. *Meat Science*, *110*, 145–152. doi:10.1016/j.meatsci.2015.07.009

Nyafu, K. (2009). *Warthog as an introduced species in the Eastern Cape*. MSc thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

Odadi, W. O., Karachi, M. K., Abdulrazak, S. A., & Young, T. P. (2011). African wild ungulates compete with or facilitate cattle depending on season. *Science*, *333*, 1753–1755. doi:10.1126/science.1208468

Oillic, S., Lemoine, E., Gros, J. B., & Kondjoyan, A. (2011). Kinetic analysis of cooking losses from beef and other animal muscles heated in a water bath - Effect of sample dimensions and prior freezing and ageing. *Meat Science*, *88*, 338–346. doi:10.1016/j.meatsci.2011.01.001

Onyango, C. A., Izumimoto, M., & Kutima, P. M. (1998). Comparison some physical and comparison of some physical and chemical propoerties of selected game meats. *Meat Science*, *49*, 117–125.

Pieterse, E. (2006). *Effects of increased slaughter weight of pigs on pork production*. PhD dissertation, Stellenbosch University, Stellenbosch, South Africa.

Pollard, J. C., Littlejohn, R. P., Asher, G. W., Pearse, A. J. T., Stevenson-Barry, J. M., McGregor, S. K., … Prescott, J. (2002). A comparison of biochemical and meat quality variables in red deer (*Cervus elaphus*) following either slaughter at pasture or killing at a deer slaughter plant. *Meat Science*, *60*, 85–94. doi:10.1016/S0309-1740(01)00110-3

Purchas, R. W., Triumf, E. C., & Egelandsdal, B. (2010). Quality characteristics and composition of the longissimus muscle in the short-loin from male and female farmed red deer in New Zealand. *Meat Science*, *86*, 505–510. doi:10.1016/j.meatsci.2010.05.043

Purslow, P. P. (2005). Intramuscular connective tissue and its role in meat quality. *Meat Science*, *70*, 435–447. doi:10.1016/j.meatsci.2004.06.028

Quaresma, M. A. G., Alves, S. P., Trigo-Rodrigues, I., Pereira-Silva, R., Santos, N., Lemos, J. P. C., … Bessa, R. J. B. (2011). Nutritional evaluation of the lipid fraction of feral wild boar (*Sus scrofa scrofa*) meat. *Meat Science*, *89*, 457–461. doi:10.1016/j.meatsci.2011.05.005

Radder, L., & Le Roux, R. (2005). Factors affecting food choice in relation to venison: A South African example. *Meat Science*, *71*, 583–9. doi:10.1016/j.meatsci.2005.05.003

Realini, C. E., Pérez-Juan, M., Gou, P., Díaz, I., Sárraga, C., Gatellier, P., & García-Regueiro, J. A. (2013). Characterization of *Longissimus thoracis*, *Semitendinosus* and *Masseter* muscles and relationships with technological quality in pigs. 2: Composition of muscles. *Meat Science*, *94*, 417–423. doi:10.1016/j.meatsci.2013.03.007

Rehfeldt, C., Stickland, N. C., Fiedler, I., & Wegner, J. (1999). Environmental and genetic factors as sources of variation in skeletal muscle fibre number. *Basic Applied Myology*, *9*, 235–253.

Rhee, M. S., Wheeler, T. L., Shackelford, S. D., & Koohmaraie, M. (2004). Variation in palatibility and biochemical traits within and among eleven beef muscles. *Journal of Animal Science*, *82*, 534–550. doi:http://dx.doi.org/10.1108/17506200710779521

Richardson, N. J. (1994). UK consumer perceptions of meat. *The Proceedings of the Nutrition Society*, *53*, 281–287. doi:10.1079/PNS19940033

Rincker, P., & Bechtel, P. (2006). Similarities and differences in composition and selected sensory attributes of reindeer, caribou and beef. *Journal of Muscle Foods*, *17*, 65–78. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.1745-4573.2006.00036.x/full

Rødbotten, M., Kubberød, E., Lea, P., & Ueland, O. (2004). A sensory map of the meat universe. Sensory profile of meat from 15 species. *Meat Science*, *68*, 137–44. doi:10.1016/j.meatsci.2004.02.016

Ruusunen, M., & Puolanne, E. (2004). Histochemical properties of fibre types in muscles of wild and domestic pigs and the effect of growth rate on muscle fibre properties. *Meat Science*, *67*, 533–539. doi:10.1016/j.meatsci.2003.12.008

Sales, J., & Kotrba, R. (2013). Meat from wild boar (*Sus scrofa* L.): A review. *Meat Science*, *94*, 187–201. doi:10.1016/j.meatsci.2013.01.012

Shapiro, S., & Wilk, M. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, *52*, 591–611. Retrieved from http://www.jstor.org/stable/2333709

Skewes, O., Morales, R., Mendoza, N., Smulders, F. J. M., & Paulsen, P. (2008). Carcass and meat quality traits of wild boar (*Sus scrofa s*. L.) with 2n = 36 karyotype compared to those of phenotypically similar crossbreeds (2n = 37 and 2n = 38) raised under the same farming conditions 2: Fatty acid profile and cholesterol. *Meat Science*, *80*, 1200–1204. doi:10.1016/j.meatsci.2009.04.017

Somers, M. J. (1992). *The implications of social structure for conservation and control of a warthog Phacochoerus aethiopicus population in the Andries Vosloo Kudu Reserve, Eastern Cape province*. MSc Thesis, University of Pretoria, Pretoria, South Africa.

Somers, M. J., Rasa, O. A. E., & Penzhorn, B. L. (1995). Group structure and social behaviour of warthogs *Phacochoerus aethiopicus*. *Acta Theriologica*, *40*, 257–281.

Stevenson, J. M., Seman, D. L., & Littlejohn, R. P. (1992). Seasonal variation in venison quality of mature, farmed red deer stags in New Zealand. *Journal of Animal Science*, *70*, 1389–1396.

Stevenson, J. M., Seman, D. L., Weatherall, I. L., & Littlejohn, R. P. (1989). Evaluation of venison color by an objective method using CIELAB values. *Journal of Food Science*, *54*, 1661–1662.

Swanepoel, M., Leslie, A. J., & Hoffman, L. C. (2016). Farmers' perceptions of the extra-limital common warthog in the Northern Cape and Free State provinces, South Africa. *Wildlife Society Bulletin*. doi:10.1002/wsb.617.

Swanepoel, M., Leslie, A. J., & Hoffman, L. C. (2014). The influence of season and sex on the carcass yield of common warthog (*Phacochoerus africanus*). *South African Journal of Wildlife Research*, *44*, 179–188.

Szmańko, T., Górecka, J., Korzeniowska, M., Malicki, A., & Eeremenko, E. (2007). Comparison of chosen quality parameters of meat from wild boar and domestic pigs. *Polish Journal of Food and Nutrition Sciences*, *57*, 523–528.

Taylor, R. G. (2004). Connective tissue structure, function and influence on meat quality. In W. K. Jensen, D. Carrick, & M. Dikeman, M. (Eds.), *Encyclopedia of Meat Sciences* (pp. 306–314). Oxford, UK: Elsevier Ltd.

Taylor, R. G., Labas, R., Smulders, F. J. M., & Wiklund, E. (2002). Ultrastructural changes during aging in M. *Longissimus thoracis* from moose and reindeer. *Meat Science*, *60*, 321–326. doi:10.1016/S0309-1740(01)00120-6

Taylor, W. A., Skinner, J. D., & Krecek, R. C. (2005). Seasonal body condition indices of mountain reedbuck (*Redunca fulvorufula*) in two areas of South African Highveld: the grassland and Karoo biomes. *South African Journal of Animal Sciences*, *35*, 19–29. doi:10.4314/sajas.v35i1.4045

TRAFFIC, East/Southern Africa. (1997). *Food for thought: The utilization of wild meat in eastern and southern Africa*. In R. Barnett (Ed.). Nairobi, Keny: TRAFFIC Eeast/Southern Africa.

Treydte, A. C., Baumgartner, S., Heitkönig, I. M. A., Grant, C. C., & Getz, W. M. (2013). Herbaceous forage and selection patterns by ungulates across varying herbivore assemblages in a South African Savanna. *PloS One*, *8*, e82831. doi:10.1371/journal.pone.0082831

USDA National Nutrient Database for Standard Reference. (2008). Full Report (All Nutrients) 11167, Corn, sweet, yellow, raw. Release 28. Nutrient Data Laboratory, ARS, USDA. Retrieved from db.nal.usda.gov/ndb/foods.

Valencak, T. G., Gamsjäger, L., Ohrnberger, S., Culbert, N. J., & Ruf, T. (2015). Healthy n-6/n-3 fatty acid composition from five European game meat species remains after cooking. *BMC Research Notes*, *8*, 273. doi:10.1186/s13104-015-1254-1

Valencak, T., & Gamsjäger, L. (2014). Lipids in tissues of wild game : Overall excellent fatty acid composition, even better in free- ranging individuals. In P. Paulsen, A. Bauer, & F. J. M. Smulders (Eds.), *Trends in Game Meat Hygiene* (pp. 335–344). Wageningen Academic Publishers. doi:10.3920/978-90-8686-238-2

Van der Wal, P. G. ., Bolink, A. H., & Merkus, G. S. M. (1988). Differences in quality characteristics of normal, PSE and DFD pork. *Meat Science*, *24*, 79–84. doi:10.1016/0309-1740(89)90009-0

Van Schalkwyk, D. L., & Hoffman, L. C. (2010). *Guidelines for the Harvesting of Game for Meat Export*. Windhoek, Namibia: Printech.

Van Zyl, L., & Ferreira, A. V. (2004). Physical and chemical carcass composition of springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus dorcas phillipsi*) and impala (*Aepyceros melampus*). *Small Ruminent Research*, *53*, 103–109. doi:10.1016/j.smallrumres.2003.08.017

Veblen, K. E., & Young, T. P. (2010). Contrasting effects of cattle and wildlife on the vegetation development of a savanna landscape mosaic. *Journal of Ecology*, *98*, 993–1001. doi:10.1111/j.1365-2745.2010.01705.x

Voisey, P. W. (1976). Engineering assessment and critique of instruments used for meat tenderness evaluation. *Journal of Texture Studies, 7*, 11-48

Von la Chevallerie, M., Erasmus, J. M., Skinner, J. D., & Van Zyl, J. H. M. (1971). A note on the carcass composition of the common eland (*Taurotragus oryx*). *Suid Afrika Tydskrif van Natuurnavorsing*, *1*, 129–131.

Warris, P. (2000). *Meat Science*. Oxon, USA: CAB Publishing.

Wiklund, E., Andersson, A., Malmfors, G., & Lundström, K. (1996). Muscle glycogen levels and blood metabolites in reindeer (*Rangifer tarandus tarandus* L .) after transport and lairage. *Meat Science*, *42*, 133–144.

Wiklund, E., Dobbie, P., Stuart, A., & Littlejohn, R. P. (2010). Seasonal variation in red deer (*Cervus elaphus*) venison (M. *longissimus dorsi*) drip loss, calpain activity, colour and tenderness. *Meat Science*, *86*, 720–727. doi:10.1016/j.meatsci.2010.06.012

Wood, J. D., Enser, M., Fisher, A. V., Nute, G. R., Sheard, P. R., Richardson, R. I., … Whittington, F. M. (2008). Fat deposition, fatty acid composition and meat quality: A review. *Meat Science*, *78*, 343–58. doi:10.1016/j.meatsci.2007.07.019

Chapter 7

The sensory profile of *Longissimus thoracis et lumborum* of common warthog (*Phacochoerus africanus*)

Abstract

The common warthog (*Phacochoerus africanus*) has historically been hunted and consumed by rural communities throughout its distribution range in Africa, while the species currently occurs extra-limitally in parts of South Africa through deliberate introductions. Warthogs are a known agricultural pest and hunted by agricultural producers for damage reprisal, which together with recreational/commercial hunting produce a carcass that can be utilized as game meat. However, the meat from warthogs sometimes exhibits an undesirable flavour similar to boar taint or smelly/tainted meat. This study investigated the sensory, physical, and chemical attributes of warthog derived from adult and juvenile boars and sows. Overall, age appeared to have a greater influence compared to gender on the sensory attributes. An undesirable odour and flavour detected were described as "sour/sweaty" and "fishy" and were scored higher in juveniles than adults, but not for sexes between age class. Adults differed from juveniles regarding fishy (P = 0.006) and sour/sweaty aromas (P = 0.03), and chicken (P = 0.04) and fishy flavours (P = 0.05). The textural (mouth-feel) attributes also differed among the four groups, including tenderness (P = 0.0007) and residue and age (P = 0.05). In terms of the fatty acid profile, only palmitoleic (C16:1), arachidonic (C20:4ω6) and the n6:n3 ratio differed among the four groups (P = 0.06, P = 0.03, and P = 0.02, respectively). The other fatty acids were similar (P > 0.05). The influence of sex and age on physical characteristics and healthiness of warthog meat were considered negligible, which was high in protein (~32%) and low in total fat (< 2%) contents. From the results of this study, the utilization of warthog meat is proposed as a strategy to encourage warthog control and population management, with the added advantage of acquiring financial benefits and contributing to food security.

Keywords: warthog, *Phacochoerus africanus*, game meat, suid, sensory, flavour, sour, sweaty

1 Introduction

The formal production of meat from wild animals has been suggested as a low-input, high production alternative to traditional animal husbandry (Carruthers, 2005, Van Schalkwyk, McMillin, Witthuhn, & Hoffman, 2010, Kiley-Worthington, 2014). Compared to domestic livestock, wild herbivores are more efficient at converting feed, more resistant to endemic pests and pathogens, less water-dependent and more adapted to climatic extremes (Child, Musengezi, Parent, & Child, 2012, Lindsey et al., 2013). Utilizing wild animals for meat production contributes towards sustainable wildlife and habitat management, and local food security, while generating an income from a widely available resource (Barnes & de Jager, 1996, White & Lowe, 2008, Poshiwa, Groeneveld, Heitkönig, & Prins, 2013, Chaminuka, Udo, Eilers, & van der Zijpp, 2014). A global trend towards healthier and sustainable living promotes the increased production and consumption of the meat from wild animals, also referred to as game meat. Game meat is generally low in total fat and cholesterol content and high in total protein content, with a favourable fatty acid profile, compared to the meat from domestic species (Van Zyl & Ferreira, 2004, Hoffman, Kroucamp, & Manley, 2007a, Mostert & Hoffman, 2007, Hoffman, Smit, & Muller, 2008, Dannenberger, Nuernberg, Nuernberg, & Hagemann, 2013, Bartoň, Bureš, Kotrba, & Sales, 2014).

Game meat destined for the formal market is produced by farms and reserves that farm with or hunt wild animals, and is also a by-product of hunting for recreation, population management or problem animal control purposes (Lindsey, Roulet, Romañach, 2007, Van Schalkwyk et al., 2010, Lindsey et al., 2013). Foreign and local hunters pay to hunt ungulate species for biltong production (a type of South African dried meat product) and trophy animals on ranches and reserves (Van der Merwe & Saayman, 2014). The production of fresh game meat only generates a small portion of the total income generated as the meat from hunted carcasses is still relatively under-utilized by hunters and/or the commercial sector. Utilizing game meat would not only contribute towards food security but create a formal chain of game meat production for the commercial market which promotes sustainable wildlife management and utilization.

Although the formal game meat industry produces sizable quantities game meat in many southern African countries annually (Van Schalkwyk et al., 2010, Department of Agriculture, Forestry and Fisheries [DAFF], 2013), it has been suggested that general ignorance regarding the quality aspects of game meat and preparation methods has been crippling the growth of the fresh game meat industry (Chapter 2). According to Bender (1992) meat consumption is primarily influenced by availability, price and tradition. However, it is also possible that consumers associated game meat with lower quality and flavour attributes and therefore desirability, while they might also be unfamiliar with game meat species. For example, the appearance of game meat colour has been considered unattractive by consumers (Volpelli, Valusso, Morgante, Pittia, & Piasentier, 2003, Hoffman & Wiklund, 2006, Hoffman et al., 2007a, Hoffman & Laubscher, 2010). Burger (2002) found that black consumers for example were more concerned about the "strong flavour" of game meat and subsequently consumed more wild-caught fish than game meat. Koster, Hodgen, Venegas, and Copeland (2010) found hunters tended to prefer animal species they associate with an appealing flavour, and may therefor only hunt and consume the meat of a smaller number of species than those available to them, or only hunt those they are familiar with. Therefore educating consumers on the quality characteristics and preparation of game meat is necessary to encourage game meat consumption.

As mentioned in Chapter 6, a number of studies contended that game meat should be classified and marketed according to species and rearing system (wild or farmed) considering the significant differences in fatty acid composition and associated sensory characteristics (Rødbotten, Kubberød, Lea, & Ueland, 2004, Hoffman, Mostert, & Laubscher, 2009a, Valencak, Gamsjäger, Ohrnberger, Culbert, & Ruf, 2015). Therefore, it is suggested that common warthog (*Phacochoerus africanus*) also be classified as a game meat species. The warthog has historically been hunted and consumed by rural communities throughout its large distribution range across Africa, and considered as "bushmeat". Although warthog meat has not always been considered as part of the formal game meat spectrum, it is becoming more widely known and accepted as Hoffman, Muller, Schutte, Calitz, and Crafford (2005a) found warthog to be a game meat species regularly consumed in South Africa and in restaurants. Currently the species occurs extra-limitally in parts of South Africa through deliberate introductions and subsequent range expansion (Chapter 2). Warthogs are hunted by agricultural producers for damage reprisal, and by recreational and trophy hunters (Nyafu, 2009, Swanepoel, Leslie, & Hoffman, 2016, Chapter 4). This produces a carcass of which the meat can be used for human consumption. In 2013 warthogs were the 2nd most often trophy hunted animal in South Africa by foreign hunters (Professional Hunting Association of South Africa [PHASA], 2014), but it is expected that the number of warthog hunted annually is greatly under estimated as there are farmers who reportedly cull on average over 700 per annum on their respective farm.

Similar to other game species, warthogs have a high dressing percentage, low total intramuscular lipid content, high total protein and moisture content and a favourable fatty acid profile (Hoffman & Sales, 2007, Swanepoel, Leslie, & Hoffman, 2014, Chapter 5 & 6). There have been reports that the meat from warthogs sometimes exhibits a flavour that is similar to boar taint, and is often referred to as "smelly/tainted" by some local consumers. Boar taint is an undesirable odour and taste which may occur in the meat from entire male domestic pigs (*S. scrofa*), while a wild or livery flavour has also been associated with other game animal species from southern Africa. In addition, the differences in physical and chemical characteristics of skeletal muscles determine palatability and therefore consumer enjoyment and acceptance. However, no research has been conducted on the aroma or flavour of warthog meat and therefore further investigation is required to determine the sensory profile of the meat, in relation to aspects that might influence this. This study aimed to investigate the sensory and chemical profile of cooked *Longissimus lumborum* muscle of warthogs derived from juvenile and adult sows and boars.

2 Methods

2.1 Culling, slaughtering and sampling

Free-roaming warthogs were culled on the Pongola Game Reserve (27° 22' 09.26" S, 31° 50' 42.16" E) situated in KwaZulu Natal province in South Africa. A total number of 31 warthogs were shot using single shot bolt action rifles (Ethical clearance number: 11LV_HOF02), during the daylight hours in March 2015 when sighted until the desired quota per group (N = 8) was achieved. Unfortunately, only seven warthogs for the group of juvenile males were culled as the full quota could not be obtained within the given time period. Although other studies used tusk protrusion and molar eruption as the basis for classifying age classes (Mason, 1984), the data capturing team had difficulty in judging their age in the field during culling as warthogs have a secretive and avoidance behaviour towards humans/vehicles (Chapter 6), animals were shot as they were observed with a certain bias towards sex and age, as it was not desired to cull animals unnecessarily. Therefore, tusk protrusion and estimated body weight was used as a visual tool to determine age classing. In support of this decision, the animals weighing less than 35 kg, with no tusk protrusion past the flanges of the lips were classified as juveniles, and all other animals classified as mature adults.

Immediately after shooting, the animals were exsanguinated by thoracic sticking, transported to a slaughter facility and weighed and dressed according to the *Guidelines for the Harvesting of Game Meat Export* (Van Schalkwyk & Hoffman, 2010). The dead weight of the animal was defined as the total weight of the animal (minus the blood lost during exsanguination). Dressing entailed the removal of the head, feet and skin. The head was removed by making a horizontal cut between the axis and atlas bones of the neck vertebrae. The trotters were removed by making a horizontal cut through the metacarpal carpal joint (joints between the carpal joints and radius and ulna and the tibia and fibula). The skin was removed by starting at the anus and working towards the neck area, while attempting to leave as much subcutaneous fat on the carcass as possible. After evisceration the carcass was washed, allowed to drip dry for ± 20 minutes before being weighed again to determine hot carcass weight. After the carcass was stored at 4°C it was weighed again to determine cold carcass weight (24h post mortem). The *Longissimus thoracis et lumborum* (LTL) muscles excised 24 hours post-mortem from the carcass were weighed, vacuum packed and frozen at –20°C before being transported to Stellenbosch University. The left LTL was used for sensory and chemical analyses.

2.2 pH

A pH measurement was taken from the *Longissimus lumborum* muscle (~3rd last rib) ± 45 min after exsanguination using a Crison pH25 handheld portable pH meter (Lasec (Pty) Ltd, South Africa). Before each reading, the meter was calibrated with standard buffers (pH 4.0 and pH 7.0) as provided by the manufacturer. A final measurement was taken 24 hours post-mortem after the LTL had been excised and was considered as ultimate pH (pH_u).

2.3 Sample preparation

The LTL muscles were defrosted overnight (12h) at 4°C. The thawed muscles were gently dabbed dry with a paper towel and weighed to determine thaw loss. The entire excised LL muscle was then divided to roughly represent the *Longissimus thoracis* (LT) (T_3 to T_{12}/T_{13}) and *Longissimus lumborum* (LL) (T_{12}/T_{13} to L_5) portion and weighed again. The visible fat and tendons were removed before the LT portion was homogenized, vacuum packed and stored at –80°C for chemical analysis. The LL portion was vacuum packed and stored at 4°C prior to sensory analysis the subsequent day. The LL portion for sensory analysis were removed from the vacuum package, blotted dry and placed in individually marked oven bags (Glad®), and prepared according to the method described by Geldenhuys, Hoffman, and Muller (2014). After cooking to an internal core temperature of 75°C (± 45 min), the LL was removed from bags and allowed to cool for 10 minutes before being blotted dry and weighed to determine cooking loss, and subsequently cut into 1.2 cm^3 cubes which were wrapped in aluminium foil. The foil-wrapped cubes were placed in ramekins and reheated at 100°C for 7 minutes before serving. After preheating the meat was covered with petri-dish lids and placed on half-filled cups in waterbaths heated to 70°C in order to maintain temperature.

2.4 Descriptive sensory analysis

A panel of 10 judges were trained according to Lawless and Heymann (2010) using generic descriptive techniques. The panellists were recruited from a pre-existing group of judges involved with research studies on meat at Stellenbosch University. During six one hour long training sessions the panellists made use of reference samples to formulate a list of sensory attributes, including aroma, flavour and texture. The sensory attributes and reference samples are described in Table 1. The cooked samples were evaluated by the trained panellists during seven blind-tasting sessions of ± 45 minutes that scored each attribute on an unstructured 100-point scale. The cooked samples were presented to, and the data collected from, panellists using Compusense® five software (Compusense, Guelph, Canada) whilst seated in booths in a temperature (21°C) and light (artificial daylight) controlled room. Each panellists received three samples of a warthog LL randomly assigned to the session per group. The test reproducibility of the trained panel was determined using test-retest as described by Geldenhuys et al. (2014).

Table 16: Definition and scale of each attribute used for the descriptive sensory analysis of warthog *Longissimus lumborum.*

Sensory attribute	Description	Reference
Aroma*		
Pork aroma	Associated with cooked pork	Pork loin chop
Chicken aroma	Associated with cooked chicken	Chicken breast
Gamey aroma	Associated with game meat	Fallow deer loin
Sour/sweaty aroma	Associated with warthog meat	Warthog fillet
Fishy aroma	Associated with smoked fish	Smoked mackerel
Flavour*		
Pork flavour	Associated with cooked pork	Pork loin chop
Chicken flavour	Associated with cooked chicken	Chicken breast
Sour/sweaty flavour	Associated with warthog meat	Warthog fillet
Metallic flavour	Associated with heavily pigmented meat	Fallow deer loin
Gamey flavour	Associated with game meat	Fallow deer loin
Fishy flavour	Associated with smoked fish	Smoked mackerel
Texture (mouth-feel)		
Initial juiciness	Amount of fluid exuded when pressed between thumb and forefinger 0 = Dry, 100 = Juicy	Chicken breast
Sustained juiciness	Impression formed after first 5 chews using molar teeth 0 = Dry, 100 = Juicy	Chicken breast
Tenderness	Impression formed after first 5 chews using molar teeth 0 = Tough, 100 = Tender	Chicken breast
Residue	Amount of residue left in mouth after 10 chews using molar teeth 0 = None, 100 = Abundant	Pork loin chop**

*Scale for descriptors: 0 = Low, 100 = High, unless otherwise stated. Aroma and flavour were analysed orthonasally and retronasally, respectively.
**Cooked to internal temperature of 75°C.

2.5 Proximate analyses

The total moisture, ash and crude protein content (%) was determined according to the Association of Official Analytical Chemist's Standard Techniques (AOAC) method 934.01 (for moisture content), method 942.05 (for ash content) and the Dumas combustion method 992.15 (for crude protein content)

(AOAC 1992, 2002a, 2002b). Total moisture content was determined using a 2.5 g homogenized sample. The moisture-free sample was used to determine total ash content. A 0.15 g, defatted, dried and finely ground sample was used for crude protein analysis with a Leco Nitrogen/Protein Analyser (FP – 528, Leco Corporation). Before the analyses the machine was calibrated using 0.15 g ethylenediamineteraacetic acid (EDTA) samples (Leco Corporation, 3000 Lakeview Avenue, St. Joseph, MI 49085-2396, USA, Part no.502-092, Lot no. 1055). After 20-30 analyses the machine was again calibrated with EDTA samples. The percentage Nitrogen (% N) per sample was determined and multiplied by a conversion factor of 6.25 to calculate the total crude protein content per sample. The chloroform/methanol (1:2, vol/vol) extraction method as described by Lee, Trevino, and Chaiyawat (1996) was used to determine the total lipid content using a 5 g sample. The laboratory at the Department of Animal Sciences, Stellenbosch University, is accredited by the Agricultural Laboratory Association of South Africa (AgriLASA) to perform accurate and reliable proximate analyses and for validation of accuracy and repeatability, partakes in monthly inter-laboratory blind tests.

2.6 Shear force

The Warner Bratzler shear force test (WBSF) was used to determine the instrumental shear force of the cooked meat samples as described by Honikel (1998). The samples were wrapped in aluminium foil, placed in plastic bags and refrigerated at 4°C for three days (72 hrs) before being subjected to analyses. Three adjacent 1 cm x 1 cm meat strips were cut parallel to the muscle fibre direction, and cut further into a minimum of six rectangular cubes (1x1x2 cm). An Instron Universal Testing Machine attached with a Warner-Bratzler (WB) fitting (Voisey, 1976) was used to determine the shear force required to cut the meat sample perpendicularly to the muscle fibres at a crosshead speed of 200 mm/min. Shear values were recorded in Newton (N) and an average was calculated according to the number of samples.

2.7 Fatty acid analysis

Total lipids were extracted according to the method described by Folch, Lees, and Sloane-Stanley (1957). Chloroform/methanol (1:2, vol/vol) solution was used for extraction of a 2 g homogenized sample. The extraction solution contained 0.01 % butylated hydroxytolene (BHT) to act as an anti-oxidant. A 2 g meat sample and 20 ml solution was homogenized using a polytron mixer (Kinematica, type PT 10–35, Switzerland). Heptadecanoic acid (C17:0) was added (0.5 ml) to the homogenized sample as an internal standard in order to quantify the observed fatty acids in the sample (Internal standard: Catalogue number H3500, Sigma-Aldrich Inc., 3050 Spruce Street, St. Louis, MO 63103, USA). A 250 µL sub-sample of the extraction was transmethylated for 2 h at 70°C in a water-bath using methanol/sulphuric acid (19:1, vol/vol) as transmethylating agent (2 ml). The transmethylated sample was cooled to room temperature before the fatty acid methyl esters (FAME) were extracted by adding

1 ml dH2O and 2 ml hexane to the sample and transferring the top hexane layer. The sample was dried under nitrogen, after which 50 µL hexane was added, of which 1 µL was injected into the gas chromatograph. The FAMEs were analysed using a Thermo TRACE 1300 series gas-chromatograph (Thermo Electron Corporation, Milan, Italy) equipped with a flame-ionisation detector, using a 30 m TR-FAME capillary column with an internal diameter of 0.25 mm and a 0.25 µm film (Cat. No. HY260M142P, Anatech, Cape Town, South Africa) and a run time of *ca*. 40 mins. The following oven temperature settings were utilised: initial temperature of 50 °C (maintained for 1 min) and final temperature of 240 °C attained after three ramps (initial increase at a rate of 25 °C/min until a temperature of 175 °C was reached; thereafter an immediate increase at a rate of 1.5 °C/min to reach 200 °C and maintenance of this temperature for 6 min; lastly an increase at a rate of 10 °C/min to reach 240 °C and maintenance of this temperature for a minimum of 2 min). The injector temperature was set at 240 °C and the detector temperature at 250 °C. The hydrogen gas flow rate was 40 mL/min. The FAME of each sample was identified by comparing the retention times with those of a standard FAME mixture (Supelco™ 37 Component FAME mix, Cat no. 47885-U, Supelco, USA), with results being expressed as mg fatty acid/g meat.

2.8 Statistical analysis

The study design consisted of four treatments with age and sex as the main factors. Seven warthogs were randomly assigned to each testing session, resulting in seven replications per treatment. The sensory data was pre-analysed using the software program Panelcheck (Version 1.3.2, www.panelcheck.com) to evaluate the consistency of the sensory panel. The sensory, physical and chemical data was analysed by test-retest Analysis of variance (ANOVA) using SAS software (Statistical Analysis Software 2006, Version 9.2, SAS Institute Inc., Cary, NC, USA) to determine the reliability of the data. The normality of the data was analysed using the Shapiro-Wilk test (Shapiro & Wilk, 1965), and outliers were identified from normal probability plots, and removed where deemed necessary. Analysis of variance was performed on all the data using the GLM (General Linear Model) procedure. The model for the experimental design is indicated by the following equation:

$y_{ijk} = \mu + s_j + a_k + sa_{ik} + \varepsilon_{ijk}$

The terms within the model are defined as: the response obtained for the i^{th} observation for the j^{th} gender (y_{ijk}), the overall mean (μ), the sex main effect (s_j), the age main effect (a_k), the sex by age interaction effect (sa_{ij}) and the random error (ε_{ijk}) associated with response on the i^{th} observation in the j^{th} sex and the k^{th} age. For post hoc testing, Fisher's LSD was used when the main effects/interactions analysed were significant. A 5% level of significance was used as a guideline to explain significantl differences. Pearson's correlation was used to determine the correlation coefficients for the sensory, physical and chemical data. Principal component analyses (PCA) and discriminate analysis (DA) were performed using the correlation matrix to determine and illustrate relationships between the sensory, physical and chemical data.

3 Results

The physical measurements of the culled warthogs and chemical composition of the cooked LL muscle is presented in Table 2. There was no interaction between sex and age for the physical and chemical measurements. The dead and carcass weight of warthogs differed between sexes ($P = 0.02$ and $P = 0.05$, respectively) and ages ($P < 0.001$ and $P < 0.001$, respectively), where the adult boars were heavier than the adult sows and the adults heavier than the young warthogs, the latter did not differ between sexes, while the LTL muscle from adults were heavier (P < 0.001) than that of the juvenile warthogs. There was no sex or age effect on the thawing and cooking losses of LL whilst the adult boars had the highest shear force values ($P = 0.01$), which did not differ from that of the adults sows but differed from that of the juveniles, while sex had no effect on the shear force values of the juveniles. None of the chemical characteristics of the cooked LL differed among the four groups, and were high in protein (~32%) and low in total fat (< 2%) contents. The total moisture content was negatively correlated with total protein content (r = –0.98, $P < 0.01$), fat content (r = –0.52, $P < 0.01$) and shear force (r = –0.61, $P < 0.01$) and positively with percentage thaw loss (r = 0.48, $P < 0.01$). Shear force was positively correlated with total protein content (r = 0.60, $P < 0.01$). Cooking loss was also negatively correlated with sustained juiciness (r = -0.50, $P = 0.01$).

Table 2: The average values (± SD) of the physical measurements of warthogs and chemical composition of cooked *Longissimus lumborum* muscle according to four treatments.

Parameter	Adult females (n = 8)	Adult males (n = 8)	Juvenile females (n = 8)	Juvenile males (n = 7)
Body weight (kg)	$52.8^{b} \pm 7.80$	$63.6^{a} \pm 9.94$	$33.5^{c} \pm 4.82$	$36.8^{c} \pm 12.01$
Hot carcass weight (kg)	$26.8^{b} \pm 3.49$	$32.7^{a} \pm 6.50$	$17.7^{c} \pm 3.94$	$17.7^{c} \pm 6.40$
Cold carcass weight (kg)	$26.1^{b} \pm 3.43$	$31.8^{a} \pm 6.44$	$16.4^{c} \pm 2.73$	$17.2^{c} \pm 6.30$
Dress out (%)*	$49.6^{a} \pm 1.67$	$49.8^{a} \pm 2.88$	$49.0^{a} \pm 2.63$	$46.4^{b} \pm 3.26$
LTL weight (kg)	$0.9^{a} \pm 0.12$	$1.02^{a} \pm 0.23$	$0.7^{b} \pm 0.10$	$0.6^{b} \pm 0.20$
pH_{45}	6.21 ± 0.37	6.33 ± 0.23	6.30 ± 0.26	6.15 ± 0.21
pH_u	5.66 ± 0.10	5.63 ± 0.07	5.64 ± 0.07	5.63 ± 0.08
Thaw loss (%)	11.9 ± 2.59	11.8 ± 3.32	11.9 ± 2.52	11.2 ± 2.22
Cooking loss (%)	21.5 ± 9.72	20.4 ± 12.50	24.8 ± 9.74	21.2 ± 8.55
Shear force (N)	$31.8^{ab} \pm 8.99$	$35.3^{a} \pm 3.73$	$27.3^{b} \pm 4.40$	$25.8^{b} \pm 4.99$
Moisture (%)	65.7 ± 3.40	65.7 ± 1.54	67.2 ± 2.80	67.5 ± 2.34

Parameter	Adult females (n = 8)	Adult males (n = 8)	Juvenile females (n = 8)	Juvenile males (n = 7)
Protein (%)	33.2 ± 3.19	33.3 ± 1.54	31.7 ± 2.71	31.6 ± 2.23
Fat (%)	1.1 ± 0.31	1.2 ± 0.44	1.1 ± 0.32	1.2 ± 0.34
Ash (%)	2.2 ± 0.67	2.3 ± 0.85	2.1 ± 0.56	2.0 ± 0.64

[a-c]Least square means in the same row with different superscripts are significantly different ($P < 0.05$)
*Calculated using cold carcass weight.

The mean scores for the descriptive sensory attributes are presented in Table 3. During training, attribute descriptors used to describe the aroma and flavour pertaining to boar taint in domestic boars were considered by the panel as aroma and flavour descriptors, but not included in the final analysis as these were not detected by the panellists. The undesirable odour and flavoured detected were described as "sour/sweaty" and "fishy" and were scored higher in juveniles than adults, but not for sexes between age class. There was significant interaction between sex and age in pork aroma and sustained juiciness ($P = 0.08$ and $P = 0.1$, respectively). The adult males had a significantly higher pork aroma than the juvenile males, whilst the adult females' and juvenile females' pork aroma score did not differ from each other nor from the adult or juvenile males'. For the sustained juiciness, the opposite was noted with the juvenile males having significantly higher values than the adult males, but neither differing from the adult and juvenile females. Overall, age appeared to have a greater influence compared to gender on the other sensory attributes. Adults differed from juveniles regarding fishy ($P = 0.006$) and sour/sweaty aromas ($P = 0.03$), and chicken ($P = 0.04$) and fishy flavours ($P = 0.05$). The textural (mouth-feel) attributes also differed among the four groups, including tenderness ($P = 0.0007$) and residue and age ($P = 0.05$). The sensory profile of the four groups according to the noted attributes is illustrated in Figure 1.

The fatty acid (FA) composition of the four groups is presented in Table 4. There was no interaction between sex and age for any of the FA, while only palmitoleic (C16:1), arachidonic (C20:4ω6) and the n6:n3 ratio differed among the four groups ($P = 0.06$, $P = 0.03$, and $P = 0.02$, respectively). The other fatty acids were similar ($P > 0.05$). Saturated (SFA) and polyunsaturated (PUFA) contributed primarily to the FA composition, with palmitic (C16:0), stearic (C18:0), linoleic (C18:2ω6) and arachidonic being the dominant FA. A PCA bi-plot (Figure 2) shows the sensory profile for each animal according to physical attributes, approximate composition and FA composition, with Factor 1 explaining 30.23% of the variance. A DA plot (Figure 8.3) shows the complete (100%) separation between the age class and not sex according to the attributes. A complete correlation matrix is given in Table 5 to show the significant correlations between sensory attributes and approximate and FA composition. The panel did not detect any gamey aroma or flavour between the treatments, and therefore no results/correlations are available.

Table 3: The mean scores (± SD) for the descriptive sensory attributes of warthog *Longissimus lumborum* muscle according sex and age.

Sensory attribute	Adult female (n = 7)	Adult male (n = 7)	Juvenile female (n = 7)	Juvenile male (n = 7)
Pork aroma	$67.39^{ab} \pm 1.95$	$69.07^{a} \pm 2.01$	$67.28^{ab} \pm 2.55$	$65.89^{b} \pm 2.41$
Chicken aroma	15.59 ± 1.10	17.32 ± 3.30	14.66 ± 2.46	15.23 ± 2.34
Sour/sweaty aroma	$13.16^{ab} \pm 5.05$	$9.89^{b} \pm 2.25$	$16.18^{a} \pm 4.49$	$14.72^{a} \pm 4.99$
Fishy aroma	$2.01^{bc} \pm 1.37$	$1.63^{c} \pm 1.30$	$3.41^{ab} \pm 2.02$	$3.80^{a} \pm 1.49$
Pork flavour	67.38 ± 1.87	68.24 ± 2.11	67.16 ± 1.18	66.63 ± 1.30
Chicken flavour	$14.62^{b} \pm 1.59$	$16.82^{a} \pm 1.85$	$14.46^{b} \pm 1.17$	$15.11^{ab} \pm 2.21$
Sour/sweaty flavour	9.75 ± 3.66	10.26 ± 3.72	12.52 ± 3.16	12.00 ± 1.97
Fishy flavour	$3.05^{ab} \pm 1.41$	$2.35^{b} \pm 1.39$	$4.19^{a} \pm 1.36$	$3.25^{ab} \pm 0.88$
Metallic flavour	7.36 ± 2.17	5.86 ± 2.56	7.07 ± 2.49	7.71 ± 1.70
Initial juiciness	56.83 ± 4.49	52.24 ± 5.96	58.31 ± 6.56	58.01 ± 7.09
Sustained juiciness	$49.20^{ab} \pm 4.87$	$44.63^{b} \pm 5.38$	$48.84^{ab} \pm 7.38$	$52.17^{a} \pm 6.59$
Tenderness	$50.55^{c} \pm 4.77$	$51.90^{bc} \pm 1.92$	$56.17^{ab} \pm 3.77$	$57.64^{a} \pm 4.38$
Residue	$18.12^{ab} \pm 1.33$	$19.20^{a} \pm 3.59$	$17.41^{ab} \pm 1.80$	$16.02^{b} \pm 2.76$

$^{a\text{-}c}$Least square means in the same row with different superscripts are significantly different ($P < 0.05$).

Table 4: The average values ($mg \cdot g^{-1} \pm SD$) of the fatty acid composition of cooked warthog *Longissimus lumborum* muscle according to sex and age.

	Adult females	Adult males	Juvenile females	Juvenile males
Saturated fatty acids				
C12:0	0.04 ± 0.02	0.03 ± 0.01	0.03 ± 0.01	0.03 ± 0.01
C13:0	0.10 ± 0.06	0.12 ± 0.07	0.06 ± 0.04	0.06 ± 0.05
C14:0	0.08 ± 0.03	0.07 ± 0.03	0.07 ± 0.03	0.06 ± 0.02
C15:0	0.02 ± 0.01	0.01 ± 0.004	0.02 ± 0.01	0.02 ± 0.01
C16:0	2.71 ± 0.76	2.56 ± 0.93	2.49 ± 0.78	2.62 ± 0.97
C18:0	1.47 ± 0.39	1.67 ± 0.68	1.67 ± 0.66	1.74 ± 0.58
C20:0	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.01
C21:0	0.17 ± 0.08	0.15 ± 0.07	0.14 ± 0.06	0.15 ± 0.06
C22:0	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.01
C23:0	0.20 ± 0.08	0.17 ± 0.06	0.16 ± 0.07	0.20 ± 0.09
Monounsaturated fatty acids				
C14:1	0.03 ± 0.02	0.03 ± 0.01	0.02 ± 0.01	0.03 ± 0.01
C16:1	$0.19^{a} \pm 0.11$	$0.12^{ab} \pm 0.04$	$0.12^{ab} \pm 0.06$	$0.10^{b} \pm 0.03$
C18:1ω9c	0.10 ± 0.05	0.09 ± 0.05	0.12 ± 0.09	0.10 ± 0.08
C18:1ω9t	0.03 ± 0.03	0.02 ± 0.03	0.04 ± 0.05	0.03 ± 0.05
Polyunsaturated fatty acids				
C18:2ω6c	2.92 ± 1.25	3.64 ± 1.45	2.43 ± 1.59	3.26 ± 1.03
C18:3ω3	0.46 ± 0.24	0.54 ± 0.28	0.71 ± 0.43	0.59 ± 0.30
C20:2ω6	0.03 ± 0.01	0.03 ± 0.02	0.02 ± 0.02	0.03 ± 0.02
C20:3ω6	0.26 ± 0.09	0.31 ± 0.14	0.26 ± 0.08	0.28 ± 0.07
C20:3ω3	0.21 ± 0.05	0.22 ± 0.08	0.24 ± 0.08	0.27 ± 0.09
C20:4ω6	$1.15^{ab} \pm 0.56$	$1.21^{a} \pm 0.56$	$0.70^{b} \pm 0.32$	$0.92^{ab} \pm 0.26$
C20:5ω3	0.31 ± 0.14	0.35 ± 0.14	0.35 ± 0.15	0.43 ± 0.13
C22:6ω3	0.23 ± 0.10	0.20 ± 0.09	0.19 ± 0.06	0.23 ± 0.06
SFA	4.81 ± 1.20	5.09 ± 1.88	4.65 ± 1.53	4.94 ± 1.62
MUFA	0.35 ± 0.11	0.27 ± 0.12	0.30 ± 0.14	0.29 ± 0.15
PUFA	5.78 ± 2.13	6.81 ± 2.54	4.91 ± 2.44	6.42 ± 2.10
PUFA:SFA	1.21 ± 0.38	1.36 ± 0.24	1.11 ± 0.60	1.34 ± 0.31
ω6:ω3	$3.38^{ab} \pm 1.42$	$3.64^{a} \pm 1.34$	$2.19^{b} \pm 0.77$	$2.65^{ab} \pm 0.93$

[a-b]Least square means in the same row with different superscripts are significantly different ($P < 0.05$).

Table 5: Correlation matrix between the sensory attributes, proximate composition and fatty acid composition of warthog *Longissimus dorsi*.

Variables*	Pork aroma	Chicken aroma	Sour/sweaty aroma	Fishy aroma	Initial juiciness	Pork flavour	Chicken flavour	Sour/sweaty flavour	Fishy flavour	Sustained juiciness	Tenderness	Residue	Metallic
C12:0	-0.204	-0.225	-0.001	0.099	-0.081	-0.035	-0.295	-0.201	0.054	0.005	0.024	-0.138	0.087
C13:0	**0.498**	0.219	**-0.697**	**-0.725**	**-0.398**	0.287	0.112	-0.337	0.004	**-0.407**	**-0.509**	**0.465**	-0.330
C14:0	-0.028	-0.114	-0.108	0.073	**-0.406**	0.026	-0.055	-0.089	-0.084	-0.341	-0.302	0.207	0.008
C15:0	-0.123	-0.222	0.166	0.353	-0.150	-0.108	-0.066	0.227	0.152	-0.164	0.077	-0.029	0.232
C16:0	0.018	-0.143	-0.063	0.108	**-0.388**	0.098	-0.093	0.023	0.105	**-0.428**	-0.321	0.301	0.209
C18:0	-0.053	-0.214	0.015	0.188	-0.286	0.068	-0.144	0.156	0.252	-0.356	-0.145	0.271	0.241
C20:0	0.132	0.288	-0.151	0.187	-0.110	0.007	0.317	0.096	-0.294	-0.297	-0.033	0.266	-0.005
C21:0	0.045	-0.027	**-0.386**	-0.327	**-0.417**	0.147	0.023	**-0.529**	0.049	-0.189	-0.205	0.221	-0.305
C22:0	-0.064	0.015	-0.219	-0.070	**-0.419**	0.018	-0.063	-0.330	0.229	-0.310	-0.160	0.211	-0.023
C23:0	-0.163	-0.221	-0.133	-0.048	-0.205	0.047	-0.182	-0.351	0.140	-0.035	-0.038	0.051	-0.061
C14:1	0.062	0.011	-0.378	-0.322	**-0.450**	0.085	0.026	**-0.509**	0.046	-0.190	-0.184	0.203	-0.345
C16:1	0.151	0.064	-0.230	-0.148	-0.350	0.083	-0.019	0.027	-0.143	**-0.420**	**-0.620**	**0.398**	0.028
C18:1ω9c	-0.316	**-0.418**	0.194	0.344	0.059	-0.145	-0.379	0.021	0.147	0.167	0.219	-0.082	0.055
C18:1ω9t	-0.306	**-0.432**	0.301	**0.468**	0.168	-0.218	**-0.383**	0.197	0.077	0.258	0.318	-0.115	0.021
C18:2ω6c	0.335	0.215	**-0.499**	**-0.540**	**-0.459**	0.311	0.249	-0.199	0.069	**-0.438**	-0.358	**0.401**	-0.260
C18:3ω3	0.121	0.135	-0.115	0.151	-0.276	-0.016	0.220	0.171	-0.120	-0.331	-0.256	0.256	0.037
C20:2ω6	0.276	0.197	**-0.400**	-0.341	**-0.438**	0.234	0.230	-0.048	0.053	**-0.487**	**-0.415**	**0.408**	-0.123
C20:3ω6	0.058	-0.117	-0.314	-0.307	-0.327	0.262	-0.058	-0.209	0.213	-0.316	-0.197	0.331	-0.082
C20:3ω3	0.001	-0.064	-0.185	0.044	**-0.411**	0.118	0.012	-0.034	0.227	-0.355	-0.146	0.210	-0.026
C20:4ω6	**0.267**	**0.184**	-0.463	-0.578	-0.359	0.260	0.082	-0.278	0.074	**-0.412**	**-0.453**	0.348	-0.142
C20:5ω3	**0.192**	**0.110**	**-0.448**	-0.392	-0.474	0.320	0.127	-0.319	0.215	-0.296	-0.120	0.273	-0.260
C22:6ω3	**0.072**	**0.002**	-0.414	-0.400	-0.381	0.244	-0.009	**-0.424**	0.118	-0.253	-0.212	0.236	-0.243

Variables*	Pork aroma	Chicken aroma	Sour/sweaty aroma	Fishy aroma	Initial juiciness	Pork flavour	Chicken flavour	Sour/sweaty flavour	Fishy flavour	Sustained juiciness	Tenderness	Residue	Metallic
SFA	0.015	-0.128	-0.100	0.121	**-0.392**	0.099	-0.068	0.028	0.120	**-0.447**	-0.271	0.338	0.180
MUFA	-0.143	-0.296	-0.022	0.165	-0.218	-0.070	-0.312	0.004	0.012	-0.140	-0.223	0.213	-0.003
PUFA	0.313	0.210	**-0.500**	**-0.455**	**-0.514**	0.286	0.242	-0.176	0.057	**-0.508**	**-0.420**	**0.443**	-0.208
PUFA:SFA	0.207	0.372	-0.261	**-0.448**	-0.076	0.212	0.297	-0.233	0.013	-0.060	-0.102	-0.020	-0.143
n-6	0.317	0.200	**-0.502**	**-0.561**	**-0.448**	0.311	0.203	-0.229	0.080	**-0.446**	**-0.392**	**0.402**	-0.232
n-3	0.166	0.145	-0.279	0.007	**-0.455**	0.101	0.235	0.032	-0.025	**-0.444**	-0.306	0.352	-0.058
n-6:n-3	0.157	0.232	-0.195	**-0.503**	0.032	0.109	0.088	-0.269	-0.093	0.030	-0.109	-0.043	-0.108
Moisture (%)	**-0.549**	**-0.472**	**0.700**	**0.629**	**0.786**	**-0.516**	-0.322	**0.420**	0.095	**0.700**	**0.688**	**-0.463**	0.309
Protein (%)	**0.560**	**0.515**	**-0.698**	**-0.653**	**-0.745**	**0.511**	0.358	**-0.456**	-0.127	**-0.647**	**-0.653**	**0.407**	**-0.378**
Fat (%)	0.236	0.054	**-0.415**	-0.247	**-0.596**	0.279	0.134	-0.129	0.132	**-0.602**	**-0.450**	**0.508**	-0.054
Ash (%)	0.309	0.005	**-0.402**	**-0.469**	**-0.545**	**0.374**	0.101	-0.202	0.005	**-0.429**	**-0.467**	**0.426**	-0.273
Shear force (N)	0.323	**0.409**	**-0.393**	-0.338	**-0.435**	0.273	0.166	-0.094	-0.300	**-0.581**	**-0.622**	**0.470**	-0.012

*Correlation values in bold within the same row indicate significant differences (P < 0.05).

Values in bold have a p-value of > 0.5.

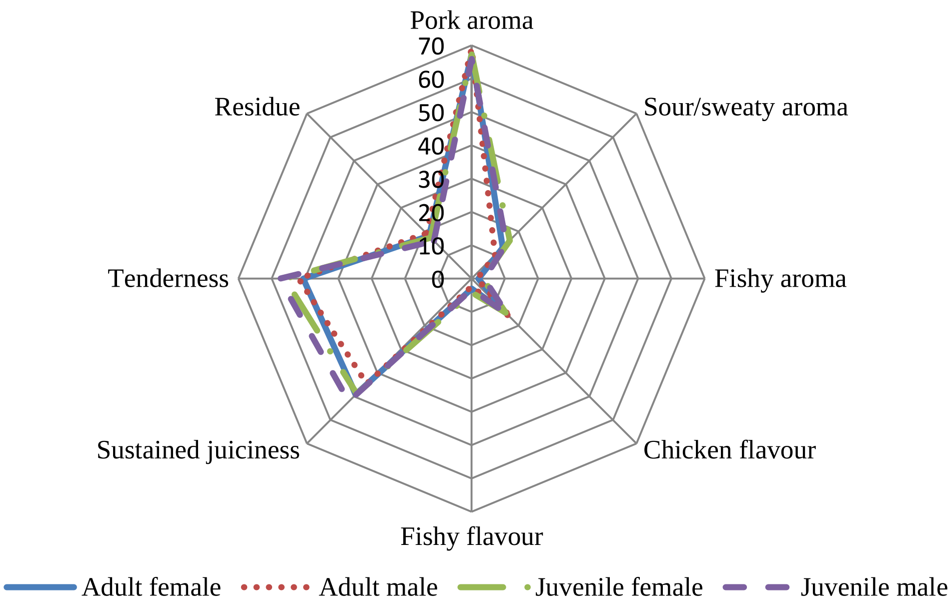

Figure 19: Spider plot illustrating the sensory attributes of the warthog *Longissimus lumborum* muscle according to four treatments.

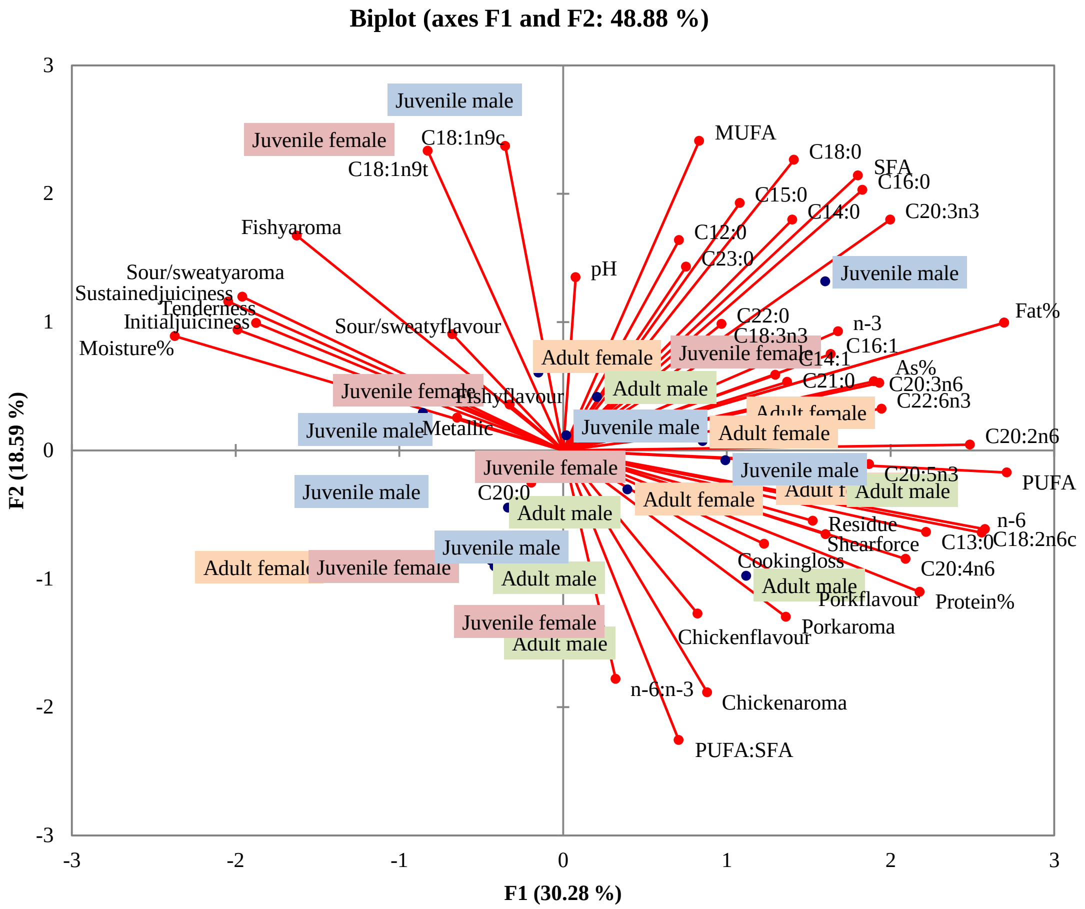

Figure 17: The PCA bi-plot of sensory attributes, physical attributes, proximate composition and fatty acid composition of warthog *Longissmus lumborum* muscle according to sex and age.

a

b

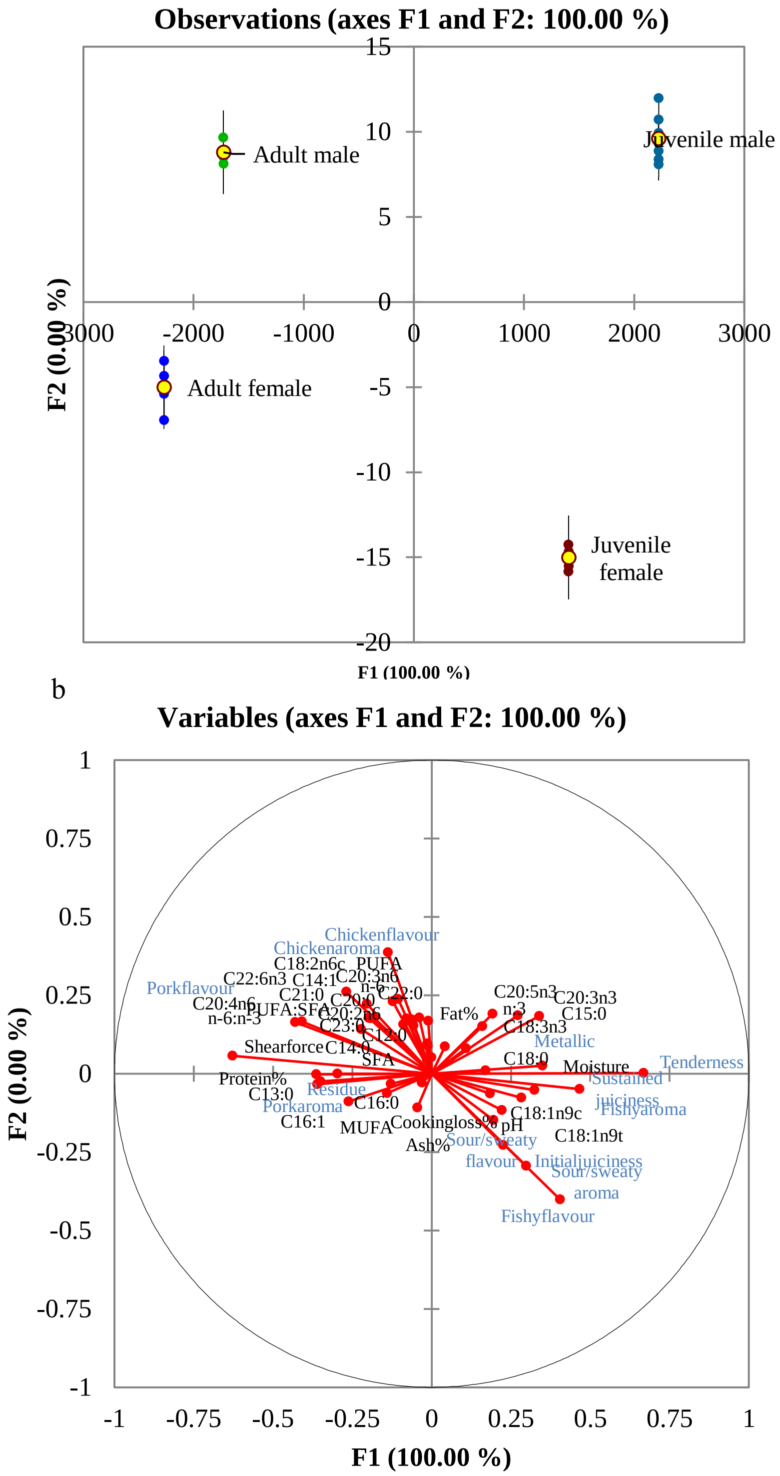

Figure 18: a) DA plot illustrating the classification of warthog *Longissmus lumborum* muscle according to sex and age based on sensory attributes, physical attributes, proximate composition and fatty acids, b) PCA bi-plot indicating the means for all these factors according to sex and age.

4 Discussion

The sensory profile of warthog meat was dominated by pork aroma and flavour and to a much lesser degree by chicken aroma and flavour, sour/sweaty aroma and fishy aroma, while the major difference in sensory profile was between ages and not between sexes. The development and growth of domestic animals progress in waves in the body according to its importance for the animal's needs, with the loin being the last region to develop (Lawrie & Ledward, 2006). Skeletal muscles are a filamentous, multinucleated combination of heterogeneous myofibres which differs in metabolic and contractile characteristics, while muscle fibre type and composition is influenced by sex, maturity, plane of nutrition and environmental conditions, among others (Keeton & Eddy, 2004). In general, the muscles from mature animals are heavier with higher fat and lower moisture, while there is an increase in the amount of non-reducible cross-links of collagen resulting in a decrease in collagen breakdown, which along with an increase in the insolubility of the muscle elastin, contributes to the overall increase in meat toughness with age (Karlsson & Klont, 1999, Purslow, 2005, Dai et al., 2009). In addition, myofibre diameter also increases with animal growth which has been negatively associated with meat tenderness, as shown by Taylor, Labas, Smulders, and Wiklund (2002) for moose and reindeer meat. Myofibre coarseness is higher in mature animals and in males (Lawrie & Ledward, 2006), but there was no difference in warthog LL tenderness between the sexes within age class. It is suggested that differences in muscle structure and composition between the adults and juveniles influence the development of aromatic compounds during cooking, as Spanier, Vercellotti, and James (1992) determined meat structure and composition act as a barrier influencing heat penetration and diffusion of water molecules during cooking, thereby creating micro-flavour environments. From Figure 3, the LL from adults are associated with meaty flavours including pork and chicken flavour, while the LL from juveniles associate with sour/sweaty and fishy flavour, and juiciness.

No differences were found here in the chemical composition between sex and age for the LL after cooking, with the chemical composition comparable to that of lean domestic and game animal meat when corrected for the effect of cooking (Gunter, & Hautzinger, 2010, North & Hoffman, 2015). Although the total fat content is inversely related to both total moisture and protein content in the meat from domestic animals, Neethling, Hoffman, and Britz (2013) contested that the overall low fat content of game meat appears to amplify the relationship between moisture and protein content. In consideration, the nitrogen, total IMF, and fatty acid profile differ among animal muscles and species, which changes with age and maturation (Lawrie & Ledward, 2006). The IMF content of warthog meat found by other studies was also low (Table 6). Even though the warthogs from this investigation had a minimum of subcutaneous fat (data not given), earlier observations (Swanepoel et al., 2014, Chapter 5) has shown that warthogs can develop a significant subcutaneous fat cover depending on season and food availability. The warthogs from this investigation were harvested at the end of summer in a summer rainfall region when it would have been expected that they would be fat, however this region was in a long drought period which would have resulted in low lipid levels in the muscles.

There were no positive associations between the sensory attributes and IMF or FA contents (Table 5), apart from an association between pork aroma and tridecanoic acid (C13:0) and elaidic acid (C18:1n9t) and fishy aroma. The composition of IMF and FA is considered to be the main driver of species-specific flavour of meat, which is primarily influenced by diet in monogastric animals (Neethling, Hoffman, & Muller, 2016). Although all meat possess the desirable 'meaty' aroma and flavour, the sensory descriptors 'gamey' and 'livery' are the most suited to discriminate among the meat from different species as they differ in intensity (Rødbotten et al., 2004). Meaty, or umami flavours are associated with amino acids, inosine monophosphate (IMP) and peptides, and sour flavours with organic acids coupled with amino acids. The meat from South African wild animals is considered to have more distinct gamey and livery flavours, and the meat from wild boars has also been associated with a gamey flavour (Lammers, Dietze, & Ternes, 2009) and considered lower in overall desirability compared to domestic pigs and pig/wild boar crosses (Sales & Kotrba, 2013).

The IMF is generally low in the meat of game species (Neethling et al., 2016), which primarily consists of structural lipid components, phospholipids and cholesterol, with high proportions of PUFA (Fisher et al., 2000). As PUFA oxidize more readily than SFA, meat high in total PUFA is more susceptible to lipid oxidation (Faustman, Sun, Mancini, & Suman, 2010) and the development of associated off-aromas and flavours which decreases meat quality and desirability. The PUFA and n-3 content in particular have been associated with gamey aroma and flavour in game meat (Hoffman, Kroucamp, & Manley, 2007b, Geldenhuys et al., 2014). In addition, game meat is typically considered a red meat due to high levels of myoglobin in wild animal muscles (Onyango, Izumimoto, & Kutima, 1998), which vary among species according to muscle fibre composition, muscle type, animal age, diet and exercise (Lawrie & Ledward, 2006). The iron content of the muscles from wild animals is subsequently also higher compared to domestic species (Hoffman, Kritzinger, & Ferreira, 2005b, Lawrie & Ledward, 2006, Nair, Suman, Li, Joseph, & Beach, 2014), while meat with high levels of UFA are more susceptible to lipid oxidation by pro-oxidants such as ferrous iron (Fe^{2+}) (Tichivangana & Morrissey, 1985).

While warthog meat is traditionally considered a game meat, there was no gamey aroma or flavour detected by the panel, and neither total PUFA nor n-3 content of warthog meat resulted in gamey attributes being detected by the panel. Although it was not measured here, the colour of uncooked warthog LL as determined in Chapter 6 was lighter (mean L* = 44.6) and less red (a* = 8.0) compared to the values found for venison and other game meats which are as typically dark red (L* < 40 and a* > 10) and considered unattractive by consumers (Volpelli et al., 2003, Hoffman & Wiklund, 2006, Hoffman et al., 2007a, Hoffman & Laubscher, 2010). Onyango et al. (1998) found an inverse relationship between L* and myoglobin content in certain game meats, and muscles with lower quantities of myoglobin and ferrous iron could affect lipid oxidation and therefore the flavour profile. This raises an interesting conundrum of whether gamey as a sensory attribute should be described as an aroma and flavour associated with game meat, since warthogs are considered a game species but produces meat without detectable gamey flavour. This also questions the findings of Rødbotten et al. (2004) regarding aptness of gamey and liver-like descriptors to distinguish among spieces, as neither were associated with warthog meat.

Diet and/or feeding regime affects IMF and FA composition and therefore volatile compounds and concentration, which in turn affects the olfactory profile more than the presence/absence of specific compounds (Pugliese & Sirtori, 2012). Pork flavour is associated with unsaturated FA, higher levels of oxidation and the subsequent development of off-aromas and flavours, which does not necessarily decrease flavour intensity or consumer desirability (Melton, 1990). Hydrocarbons, aldehydes, ketones and alcohols derived from thermal degradation and Maillard reactions are primarily associated with pork flavour, and to a lesser extent, pyrazines, furans, and pyradines (Timón, Carrapiso, Jurado, & van de Lagemaat, 2004). Pyrazines in particular are the main components of meat volatiles, while aldehydes have the highest concentration in fried pork (Lammers et al., 2009). Aldehydes are derived from PUFA during cooking and are known to contribute to the accepted pork aroma and flavour, while consumers' satisfaction with pork taste is the most important factor that determines overall satisfaction (Resano et al., 2011). Lammers et al. (2009) found the pyrazine concentrations were significantly higher in the fried meat from wild boar compared to domestic pig, and suggested that the free water content influences the pyrazines formed during the Maillard reaction, as lower amounts of free water available results in higher temperatures which favour the Maillard reaction. However, the authors did not attempt to explain the lower free water content of the wild boar meat, as it is known that moisture holding capacity and loss is influenced by rate of pH decline and pH_u, species, sex, harvesting season and culling method in wild animals. Moisture content and availability could therefore affect aromatic volatiles and flavour profile.

Variation in pH_u affects the tenderness, colour, water-holding capacity and ageing process of meat (Honikel, 2004). In domestic pigs slaughtered without ante-mortem stress a normal pH_u range between 5.5 and 5.7 is typical, and the pH_u of LL from both sexes and age class fell within this range. Daszkiewicz, Janiszewski, and Wajda (2009) agreed with others that meat from wild animals have lower pH_u possibly from increased post mortem lactic acid production compared to domestic animals. Alternatively, it could also be argued that wild animals are generally subjected to less ante-mortem stress (Kritzinger, Hoffman, & Ferreira, 2004, Hoffman & Laubscher, 2010) whilst farmed livestock species usually experience some stress during the loading, transport, lairage and stunning activities in formal abattoirs. In support, an overview of African game meat profiles found no species to have attained a pH_u of > 5.9 when there has been a minimal level of ante-mortem stress (Onyango et al., 1998, Kritzinger et al., 2004, Rincker & Bechtel, 2006, Hoffman et al., 2009a, Hoffman, van Schalkwyk, & Müller, 2009b, Hoffman & Schalkwyk, 2011, Magwedere, Sithole, Hoffman, Hemberger, & Dziva, 2013).

Wounded animals, or animals that have been pursued for a great distance, are subjected to stress resulting in the depletion of glycogen reserves and compromised meat quality. Hoffman and Sales (2007) noted similar pale, soft and exudative (PSE) characteristics in warthog meat when subjected to acute ante-mortem stress. In PSE meat, the accelerated pH decline post-mortem combined with high temperatures leads to the denaturation of proteins, and the meat becomes pale in colour, soft in texture with decreased water-holding abilities (Monin, 2004). Therefore, the harvesting of warthogs should be conducted as ethically as possible in terms of animal welfare, as it affects both meat quality and public sentiment.

None of the descriptors Rødbotten et al. (2004) used for developing a meat map for the sensory profile of different species included sour/sweaty or fishy aromas and flavours. There have been few studies investigating the sensory profile of the meat from wild animals, while there is also a lack of standardization in the sensory descriptors used by different researchers and laboratories (Neethling et al., 2016). A fishy flavour in pork has been attributed to an increased incorporation of PUFA in muscle obtained from the diet (Melton, 1990), while Wong, Nixon, and Johnson (1975) noted aromatic compounds derived from C8, C9 and C10 SFA are associated with the disagreeable 'sweaty/sour' in mutton. The method of FA analysis used in this study was designed to detect for FA from C12:0 and higher, and therefore it is suggested that more research should be conducted in determining the origin of these aromas and flavours, and investigate the occurrence of this aroma/flavour in other species. Juveniles scored higher than adults for the sour/sweaty and fishy aroma and fishy flavour, while the sour/sweaty aroma and flavour was correlated with total moisture content although there were no differences in the chemical composition between sex and age class. These results are surprising as adult males have been associated with undesirable aromas and flavours by local hunters/consumers. This is probably since entire adult pigs are known to display the undesirable flavour known as 'boar taint', while wild male ungulates are also associated with 'urine-like' or 'tainted' aromas/flavours (Neethling et al., 2016). The precursors of meat flavour are divided into water soluble components and lipids, and the aromatic volatiles develop during cooking from lipid degradation and the Maillard reaction, and from interaction between the processes (Mottram, 1998). According to Tshabalala, Strydom, Webb, and De Kock (2003), the aromatic compounds in lean meat become more volatile and are readily released with water vapour, which are encountered during orthonasal analyses. This could help explain the positive associations between aromas and moisture content.

The total moisture content was also correlated with initial and sustained juiciness, as well as tenderness, and in addition to the sour/sweaty and fishy attributes, age also influenced the sustained juiciness, tenderness and residue, but not initial juiciness. During mastication, the total moisture contributes to initial juiciness, while fats stimulate saliva secretion and total fat content therefore contributes to sustained juiciness (Lawrie & Ledward, 2006). Daszkiewicz et al. (2015) found the meat from wild fallow deer had a lower pH_u (5.3), higher total fat content, a more desirable fatty acid profile (increased PUFA content), higher aroma and flavour desirability and juiciness, compared to farmed fallow deer. Here, sustained juiciness was negatively associated with total fat content ($P < 0.01$, Table 5), as were tenderness ($P = 0.02$), and it is suggested that the total moisture content possibly contributes to a greater extent for juiciness in game meat low in fat content. Other studies have also found an association between total moisture content and juiciness (Hoffman et al., 2009b, (Geldenhuys et al., 2014), between sustained juiciness and tenderness for game meats (North & Hoffman, 2015), and between a desired pH_u (~ 5.5) and juiciness and desirable flavours in mutton (Braggins, 1996). Cooking loss is generally lower in good quality meat at ideal pH_u (Lawrie & Ledward, 2006), as found here for warthog LL cooked to an internal core temperature of 75°C. Cooking methods greatly influence the eating quality of meat, and the moist heating methods used involve more moisture and lower surface temperatures (Bejerholm & Aaslyng, 2004). Cooking loss was also negatively correlated with sustained juiciness, which indicates that juiciness is affected by water holding capacity (WHC) which in turn depends on rate of pH decline and pH_u.

The WHC, cooking and drip loss values are usually correlated with rate of pH decline post-mortem and pH_u of meat (Bouton, Harris, & Shorthose, 1971), with pH_u and WHC considered significant indicators of drip loss, or exudative meat (Kušec, Kralik, Đurkin, Petričević, & Hanžek, 2007). A positive relationship between pH_u and WHC has been found for numerous game species (Onyango et al., 1998, Hoffman, Mostert, Kidd, & Laubscher, 2009c). There were no correlations found here between pH_{45}, pH_u and thaw loss or cooking loss, while only five animals had a pH_{45} below 6. In Chapter 5, some of the warthogs (n = 11) culled had a $pH_{45} < 6$ which was positively correlated with WHC and lightness (average L*), possibly indicating the meat was PSE. However, the study found was no correlation between pH_{45} and drip loss, with all the muscles having a favourable drip loss of < 5%, as a drip loss > 5% is generally associated with PSE pork (Van der Wal, Bolink, & Merkus, 1988). Hoffman and Sales (2007) noted similar PSE characteristics in warthog meat when subjected to acute ante-mortem stress. However, it could be that the potential correlation was overshadowed by the effect (damage) of the freezing process (Leygonie, Britz, & Hoffman, 2012).

In general, tender meat is associated with a normal rate of pH decline within the desired temperature range of 10–15°C with the onset of rigor. Low pH_u values around 5.5 have been positively associated with increased tenderness compared to intermediate pH_u values ranging from 5.8-6.0 for game meat (Hoffman et al., 2007a, Wiklund, Dobbie, Stuart, & Littlejohn, 2010,) and beef (Lomiwes, Farouk, Wu, & Young, 2014). The meat from wild animals appears to have a higher initial tenderness compared to beef (Farouk, Beggan, Hurst, Stuart, Dobbie, & Bekhit, 2007, Hoffman et al., 2007a, Hoffman, Smit, & Muller, 2010, Wiklund et al., 2010, Daszkiewicz, Kubiak, Winarski, & Koba-Kowalczyk, 2012, Sales & Kotrba, 2013). The average shear force values found here were lower compared to the general threshold for beef where tenderness is denoted to shear force values < 42.28 (N) (Destefanis, Brugiapaglia, Barge, & Dal Molin, 2008). It has been suggested that post mortem proteolysis occurs at a faster rate in the muscles of game animals from the earlier activation of calpain I and calpain II post mortem compared to beef, which contribute to the tenderness associated with game meat (North, Frylinck, & Hoffman, 2015, 2016), while Daszkiewicz et al. (2009) suggested that meat tenderness might be species specific. Overall, the tenderness of warthog LL was high but differed among age groups, being higher in juveniles compared to adults. As noted by Neethling et al. (2016), tenderness is influenced by intrinsic and extrinsic biological factors, as well as storage and cooking methods. For example, the rate and method of freezing may influence moisture loss and tenderness of meat (Leygonie et al., 2012).

Palmitic, stearic, oleic (monounsaturated), and linoleic acids are the major fatty acids found in animal meat (Enser, Hallett, Hewitt, Fursey, & Wood, 1996). Here, the most abundant fatty acids of the warthog LT were palmitic and stearic (saturated) and linoleic and arachidonic (polyunsaturated) fatty acids. The level of oleic acid, and MUFA in general (Table 4), was particularly low for warthog meat (0.7%) compared to other studies, which found oleic proportions of 15.8% (C18:1n9 *cis* and *trans*) (Hoffman & Sales, 2007), 9.0% (Crawford, Gale, & Woodford, 1970) and 15.0% (Chapter 6, Table 6). As the accumulation of fatty acids in the adipose tissue increases over time (and therefore age), the MUFA content increases as the SFA content decreases from the continuing desaturation of SFA to their MUFA counterparts (Wood et al., 2008), with oleic acid the product of desaturated stearic acid.

Feeding pigs a diet high in oleic acid also increases the content of this FA in adipose tissue (Klingenberg, Knabe & Smith, 1995). In Chapter 6, a number of warthogs culled had a large quantity of maize (*Zea mays*) in their stomachs. The study did not find any differences in the FA profile of the warthogs between 'maize-filled stomachs' and 'grass-filled stomachs', but it is suggested that the consumption of maize resulted in the high MUFA content found in warthog LL in Chapter 6. Quaresma et al. (2011) found a higher total SFA and MUFA, and lower total PUFA content for feral wild boar culled on farms in Portugal, and attributed this to the abundance of acorns in autumn and winter seasons, which are high in oleic, linoleic and palmitic acids.

In general, the meat from free-ranging grazers have a higher PUFA, and n-3 in particular, content compared to farmed animals fed concentrate diets, as animals extensively feeding on grasses incorporate more n-3 and n-6 PUFA fatty acids in their muscles (Valencak & Gamsjäger, 2014). Fine and Davidson (2008) found that the FA profile of free ranging pigs (*Sus scrofa*) did not differ significantly to that from warthogs (Table 6), although it is uncertain where the warthogs were sourced from. The warthogs sampled by Crawford et al., (1970) were sourced from the Queen Elizabeth National Park in Uganda, where their diet tends to consist of 80-90% grass (Harris & Cerling, 2002). Although the contribution of arachidonic acid to total FA was high in this study, the contents were still lower compared to those found in domestic species (Enser et al., 1996) but higher than those found in Chapter 6. Arachidonic acid is an important product of linoleic and linolenic acids which are essential FA since they are obtained solely from the diet. Linoleic and γ-linolenic (and palmitic) acids are the major FA of grasses (Dungait, Docherty, Straker, & Evershed, 2010), and the intake and composition of these fatty acids may therefor differ in wild herbivore muscle due to the seasonal and regional variability of grasses.

The difference in arachidonic acid content most likely resulted in the different n-6:n-3 ratios among the four groups. The n-6:n-3 ratio is typically higher for domestic pigs compared to ruminants, as in monogastric animals PUFA pass unchanged through the gastric system to be incorporated into tissues, resulting in higher proportions (Jenkins, 1993). This does however not affect the healthy profile of warthog meat. A PUFA:SFA ratio of ≥ 0.45 and omega 6:omega 3 ($\omega 6:\omega 3$) of ≤ 4 is recommended for the meats consumed by humans (Warris, 2000) as a diet high in unsaturated FA provides health benefits. The meat from game animals generally adheres to this recommendation (Hoffman et al., 2010, Valencak & Gamsjäger, 2014, Valencak et al., 2015) and therefore appeals to the modern day consumer aware of the health attributes of game meat (MacMillan & Phillip, 2008). This was also found of the warthog LL among all sexes and age class.

Table 6: The fatty acids composition (%) of warthog muscle as found in this study and in literature.

Species	Muscle	SFA %	MUFA %	PUFA %	Total fat %	Area
Warthog	*Longissimus thoracis*[a]	41.3	2.4	56.3	1.15	KwaZulu Natal
	Longissimus lumborum[b]	40.7	28.7	30.7	1.50	Free State
	Longissimus dorsi[c]	35.8	16.7	47.6	1.69	KwaZulu Natal
	Leg muscle[d]	31.5	10.3	56	2	Uganda
	Unspecified[e]	27.8	32.6	32.4	1.29	South Africa
Free range domestic pig	*Longissimus dorsi*[f]	27.1	19.6	53.8	-	Europe (Spain)
Free range wild boar	*Longissimus dorsi*[g]	34.5	40.7	24	4.65	Portugal

[a]This study.
[b]Chapter 6.
[c]Hoffman and Sales (2007).
[d]Crawford, Gale, and Woodford (1970).
[e]Fine and Davidson (2008).
[f]Muriel, Ruiz, Ventanas, and Antequera (2002).
[g]Quaresma et al. (2011).

5 Conclusion

It is suggested that the sensory profile of warthog meat warrants further investigation as the occurrence of undesirable flavours needs to be investigated and quantified as it could influence consumer acceptance and utilization of warthog meat. Sex and age significantly influenced the sensory profile of warthog meat, while the influence of these factors on physical characteristics and healthiness of the meat are considered negligible. It is proposed that total moisture content is an important factor influencing the sensory profile and mouth-feel experience of warthog meat considering the overall low total fat. The most surprising results were that the undesirable aroma and flavour described here as “sour/sweaty” was not found only in adult males as opposed to popular belief. In addition, the sensory profile of the meat was dominated by pork aroma and flavour and not described as being gamey. This raises the question of whether gamey attributes should be described as ‘associated with game meat’, and its aptness to distinguish among meat from different species In order to elucidate on the sensory profile of warthog meat as affected by sex and age found in this study, it is suggested that the associated aromatic volatiles be determined in relation to the different FA derived compounds and amino acid composition. Therefore, to encourage the knowledge and utilization of warthog meat it is necessary to increase the research effort on its sensory profile, and the influence of factors not investigated in this study, namely diet, season, production region, and storage and preparation methods. Increased utilization of warthog meat has been proposed as a strategy to encourage warthog control and population management, and it should be considered whether the meat should be produced and marketed according to the potentially influential factors on consumers acceptance.

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7 References

AOAC International (2002a) Official methods of analysis. Arlington, Virginia, USA: Association of Official Analytical Chemists Inc. Loss on drying (moisture) at 95–100°C for feeds. (17th ed.) AOAC Official Method 934.01.

AOAC International (2002b) Official methods of analysis. Arlington, Virginia, USA: Association of Official Analytical Chemists Inc. (17th ed.). Ash of Animal Feed. AOAC Official Method 942.05

AOAC Official Method 992.15 (1992). Crude protein in meat and meat products including pet foods. Combustion method. *Journal of Association of Official Analytical Chemists International*, 76, 787.

Barnes, J. I., & de Jager, J. V. (1996). Economic and financial incentives for wildlife incentives on private land in Namibia and the implications for policy. *South African Journal of Wildlife Research*, *26*, 1–24.

Bartoň, L., Bureš, D., Kotrba, R., & Sales, J. (2014). Comparison of meat quality between eland (*Taurotragus oryx*) and cattle (*Bos taurus*) raised under similar conditions. *Meat Science*, *96*, 346–52. doi:10.1016/j.meatsci.2013.07.016

Bejerholm, C. & Aaslyng, M. D. (2004). Cooking of meat. In W. K. Jensen, D. Carrick, & M. Dikeman. (Eds.), *Encyclopedia of meat sciences* (pp. 343–349). Oxford, UK: Elsevier Ltd.

Bender, A. (1992). Meat and meat products in human nutrition in developing countries. FAO and INPhO, Food and Nutrition Paper 53. Rome, Italy: Food and Agriculture Organization of the United Nations. Retrieved from http://www.fao.org/docrep/t0562e/t0562e00.HTM.

Bouton, P. E., Harris, P. V, & Shorthose, W. R. (1971). Effect of ultimate pH upon the water-holding capacity and tenderness of mutton. *Journal of Food Science*, *36*, 435–439.

Braggins, T. J. (1996). Effect of stress-related changes in sheepmeat ultimate pH on cooked odor and flavor. *Journal of Agricultural and Food Chemistry*, *44*, 2352–2360. doi:10.1021/jf960136+

Burger, J. (2002). Daily consumption of wild fish and game: exposures of high end recreationists. *International Journal of Environmental Health Research*, *12*, 343–54. doi:10.1080/0960312021000056393

Carruthers, J. (2005). “ Wilding the farm or farming the wild ”? The evolution of scientific game ranching in South Africa from the 1960s to the present. *Transactions of the Royal Society of South Africa*, *63*, 160–181.

Chaminuka, P., Udo, H. M. J., Eilers, K. C. H. A. M., & van der Zijpp, A. (2014). Livelihood roles of cattle and prospects for alternative land uses at the wildlife / livestock interface in South Africa. *Land Use Policy*, *38*, 80–90. doi:10.1016/j.landusepol.2013.10.007

Child, B. A, Musengezi, J., Parent, G. D., & Child, G. F. T. (2012). The economics and institutional economics of wildlife on private land in Africa. *Pastoralism: Research, Policy and Practice*, *2*, 18. doi:10.1186/2041-7136-2-18

Crawford, M. A., Gale, M. M., & Woodford, M. H. (1970). Muscle and adipose tissue lipids of warthog, *Phacochoerus aethiopicus*. *International Journal of Biochemistry*, *1*, 654–658. doi:10.1016/0020-711x(70)90039-x

Dai, F., Feng, D., Cao, Q., Ye, H., Zhang, C., & Xia, W. (2009). Developmental differences in carcass , meat quality and muscle fibre characteristics between the Landrace and a Chinese native pig. *South African Journal of Animal Sciences*, *39*, 267–273.

Dannenberger, D., Nuernberg, G., Nuernberg, K., & Hagemann, E. (2013). The effects of gender, age and region on macro- and micronutrient contents and fatty acid profiles in the muscles of roe deer and wild boar in Mecklenburg-Western Pomerania (Germany). *Meat Science*, *94*, 39–46. doi:10.1016/j.meatsci.2012.12.010

Daszkiewicz, T., Janiszewski, P., & Wajda, S. (2009). Quality characteristics of meat from wild red deer (*Cervus elaphus* L.) hinds and stags. *Journal of Muscle Foods*, *20*, 428–448. doi:10.1111/j.1745-4573.2009.00159.x

Daszkiewicz, T., Kubiak, D., Winarski, R., & Koba-Kowalczyk, M. (2012). The effect of gender on the quality of roe deer (*Capreolus capreolus* L.) meat. *Small Ruminant Research*, *103*, 169–175. doi:10.1016/j.smallrumres.2011.09.044

Daszkiewicz, T., Hnatyk, N., Dąbrowski, D., Janiszewski, P., Gugołek, A., Kubiak, D., … Koba-Kowalczyk, M. (2015). A comparison of the quality of the *Longissimus lumborum* muscle from wild and farm-raised fallow deer (*Dama dama* L.). *Small Ruminant Research*, *129*, 77–83. doi:10.1016/j.smallrumres.2015.05.003

Department of Agriculture, Forestry and Fisheries (DAFF). (2013). *South African Yearbook 2012/13: Agriculture, Forestry and Fisheries*. In A. Vermeulen (Ed.) (pp 44–82). Pretoria, South Africa: Department of Agriculture, Forestry and Fisheries. Retrieved from http://www.gcis.gov.za.

Destefanis, G., Brugiapaglia, A, Barge, M. T., & Dal Molin, E. (2008). Relationship between beef consumer tenderness perception and Warner–Bratzler shear force. *Meat Science*, *78*, 153–156. doi:10.1016/j.meatsci.2007.05.031

Dungait, J. A., Docherty, G., Straker, V., & Evershed, R. P. (2010). Seasonal variations in bulk tissue, fatty acid and monosaccharide $\delta^{13}C$ values of leaves from mesotrophic grassland plant communities under different grazing managements. *Phytochemistry*, *71*, 415–28. doi:10.1016/j.phytochem.2009.10.010

Enser, M., Hallett, K., Hewitt, B., Fursey, G. A. J., & Wood, J. D. (1996). Fatty acid content and composition of english beef, lamb and pork at retail. *Meat Science*, *42*, 443–456. doi:10.1016/0309-1740(95)00037-2

Farouk, M. M., Beggan, M., Hurst, S., Stuart, A., Dobbie, P. M., & Bekhit, A. E. D. (2007). Meat quality attributes of chilled venison and beef. *Journal of Food Quality*, *30*, 1023–1039.

Faustman, C., Sun, Q., Mancini, R., & Suman, S. P. (2010). Myoglobin and lipid oxidation interactions : Mechanistic bases and control. *Meat Science*, *86*, 86–94. doi:10.1016/j.meatsci.2010.04.025

Fine, L.-B., & Davidson, B. C. (2008). Comparison of lipid and fatty acid profiles of commercially raised pigs with laboratory pigs and wild-ranging warthogs. *South African Journal of Science*, *104*, 314–316.

Fisher, A. V, Enser, M., Richardson, R. I., Wood, J. D., Nute, G. R., Kurt, E., … Wilkinson, R. G. (2000). Fatty acid composition and eating quality of lamb types derived from four diverse breed x production systems. *Meat Science*, *55*, 141–147. doi:10.1016/S0309-1740(99)00136–9

Folch, J., Lees, M., & Sloane-Stanley, G. H. (1957). A simple method for the isolation and purification of total lipids from animal tissues. *Journal of Biological Chemistry*, *226*, 495–509.

Geldenhuys, G., Hoffman, L. C., & Muller, M. M. (2014). Sensory profiling of Egyptian goose (*Alopochen aegyptiacus*) meat. *Food Research International*, *64*, 25–33. doi:10.1016/j.foodres.2014.06.005

Gunter, H., & Hautzinger, P. (2010). Meat processing technology: For small-to medium-scale producers. Food and Agriculture Organization (FAO) of the United Nations regional office for Asia and the Pacific, Bangkok Retrieved from http://www.fao.org/docrep/010/ai407e/AI407E03.htm

Harris, J. M., & Cerling, T. E. (2002). Dietary adaptations of extant and Neogene African suids. *Journal of Zoology*, *256*, 45–54. doi:10.1017/S0952836902000067

Hoffman, L. C. (2008). The yield and nutritional value of meat from African ungulates , camelidae , rodents , ratites and reptiles. *Meat Science*, *80*, 94–100. doi:10.1016/j.meatsci.2008.05.018

Hoffman, L. C., Muller, M., Schutte, D. W., Calitz, F. J., & Crafford, K. (2005a). Consumer expectations , perceptions and purchasing of South African game meat. *South African Journal of Wildlife Research*, *35*, 33–42.

Hoffman, L. C., Kritzinger, B., & Ferreira, A. V. (2005b). The effects of region and gender on the fatty acid, amino acid, mineral, myoglobin and collagen contents of impala (*Aepyceros melampus*) meat. *Meat Science*, *69*, 551–558. doi:10.1016/j.meatsci.2004.10.006

Hoffman, L. C., Kroucamp, M., & Manley, M. (2007a). Meat quality characteristics of springbok (*Antidorcas marsupialis*). 1: Physical meat attributes as influenced by age, gender and production region. *Meat Science*, *76*, 755–761. doi:10.1016/j.meatsci.2007.02.017

Hoffman, L. C., Kroucamp, M., & Manley, M. (2007b). Meat quality characteristics of springbok (*Antidorcas marsupialis*). 2: Chemical composition of springbok meat as influenced by age, gender and production region. *Meat Science*, *76*, 762–767. doi:10.1016/j.meatsci.2007.02.018

Hoffman, L. C., Mostert, A. C., Kidd, M., & Laubscher, L. L. (2009a). Meat quality of kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*): Carcass yield, physical quality and chemical composition of kudu and impala *Longissimus dorsi* muscle as affected by gender and age. *Meat Science*, *83*, 788–95. doi:10.1016/j.meatsci.2009.08.022

Hoffman, L. C., Mostert, A. C., & Laubscher, L. L. (2009c). Meat quality of kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*): The effect of gender and age on the fatty acid profile, cholesterol content and sensory characteristics of kudu and impala meat. *Meat Science*, *83*, 737–743. doi:10.1016/j.meatsci.2009.08.026

Hoffman, L. C., Van Schalkwyk, S, & Müller, N. (2009b). Effect of season and gender on the physical and chemical composition of black wildebeest (*Connochaetus gnou*) meat. *South African Journal of Wildlife Research*, *39*, 170–174.

Hoffman, L. C., & Laubscher, L. L. (2010). A comparison between the effects of day and night cropping on gemsbok (*Oryx gazella*) meat quality. *Meat Science*, *85*, 356–362. doi:10.1016/j.meatsci.2010.02.003

Hoffman, L. C., Muller, M., Schutte, D. W., Calitz, F. J., & Crafford, K. (2005). Consumer expectations, perceptions and purchasing of South African game meat. *South African Journal of Wildlife Research*, *35*, 33–42.

Hoffman, L. C., & Sales, J. (2007). Physical and chemical quality characteristics of warthog meat. *Livestock Research for Rural Development*, *19,* Article 153. Retrieved from http://www.lrrd.org/lrrd19/10/hoff19153.htm

Hoffman, L. C., Smit, K., & Muller, N. (2008). Chemical characteristics of blesbok (*Damaliscus dorcas phillipsi*) meat. *Journal of Food Composition and Analysis*, *21*, 315–319. doi:10.1016/j.jfca.2007.12.003

Hoffman, L. C., Vosloo, C., Nkhabutlane, P., & Schutte, D. W. (2005). Associations with rabbits and rabbit meat of three different ethnic groups in Stellenbosch , South Africa. *Journal of Family Ecology and Consumer Sciences*, *33*, 63–72.

Hoffman, L. C., & Wiklund, E. (2006). Game and venison – meat for the modern consumer. *Meat Science*, *74*, 197–208. doi:10.1016/j.meatsci.2006.04.005

Hoffman, L., Smit, K., & Muller, N. (2010). Chemical characteristics of red hartebeest (*Alcelaphus buselaphus caama*) meat. *South African Journal of Animal Science*, *40*, 221–228. Retrieved from http://www.scielo.org.za/scielo.php?pid=S0375-15892010000300008&script=sci_arttext

Honikel, K. O. (1998). Reference methods for the assessment of physical characteristics of meat. *Meat Science*, *49*, 447–457. doi:10.1016/S0309-1740(98)00034-5

Honikel, K. O. (2004). Conversion of muscle to meat: Glycolysis. In W. K. Jensen, D. Carrick, & M. Dikeman. (Eds.), *Encyclopedia of Meat Sciences* (pp. 314–318). Oxford, UK: Elsevier Ltd.

Jenkins, T. C. (1993). Lipid metabolism in the rumen. *Journal of Dairy Science*, *76*, 3851–3863. doi:10.1016/0079-6832(78)90004-6

Karlsson, A., & Klont, R. (1999). Skeletal muscle fibres as factors for pork quality. *Livestock Production Science*, *42*, 415–431. doi:10.1051/rnd

Keeton, J. T. & Eddy, S. (2004). Chemical and physical characteristics of meat/Chemical composition. In W. K. Jensen, D. Carrick, & M. Dikeman, M. (Eds.), *Encyclopedia of Meat Sciences* (pp. 210–218). Oxford, UK: Elsevier Ltd.

Kiley-Worthington, M. (2014). Ecological agriculture . Integrating low input , high productive farming with wildlife conservation . results from the experimental farm La Combe, Drome France. *Open Journal of Ecology*, *4*, 744–763.

Klingenberg, I. L., Knabe, D. A, & Smith, S. B. (1995). Lipid metabolism in pigs fed beef tallow or high-oleic acid sunflower oil. *Comparative Biochemistry and Physiology. Part B, Biochemistry & Molecular Biology*, *110*, 183–92. doi:10.1016/0305-0491(94)00116-C

Koster, J. M., Hodgen, J. J., Venegas, M. D., & Copeland, T. J. (2010). Is meat flavor a factor in hunters' prey choice decisions? *Human Nature*, *21*, 219–242. doi:10.1007/s12110-010-9093-1

Kritzinger, B., Hoffman, L. C., & Ferreira, A. V. (2004). A comparison between the effects of two cropping methods on the meat quality of impala (*Aepyceros melampus*). *South African Journal of Animal*, *33*, 233–241. Retrieved from http://www.ajol.info/index.php/sajas/article/view/3779

Kušec, G., Kralik, G., Đurkin, I., Petričević, A., & Hanžek D. (2007). Factors discriminating between pork quality conditions. *Poljoprivreda / Agriculture*, *13*, 66–69.

Lammers, M., Dietze, K., & Ternes, W. (2009). A comparison of the volatile profiles of frying european and australian wild boar meat with industrial genotype pork by dynamic headspace-GC/MS Analysis. *Journal of Muscle Foods*, *20*, 255–274. Retrieved from <Go to ISI>://000267283200001

Lawless, H. T., & Heymann, H. (2010). *Sensory evaluation of food: Principals and practises* (2nd ed.). New York, USA: Chapman & Hall.

Lawrie, R. A., & Ledward, D. A. (2006). *Lawrie's meat science* (7th ed.). Cambridge, England: Woodhead Publishing.

Lee, C.M., Trevino, B. & Chaiyawat, M. (1996). A simple and rapid solvent extraction method for determining total lipids in fish tissue. *Journal of AOAC International, 79*, 487–492.

Leygonie, C., Britz, T. J., & Hoffman, L. C. (2012). Meat quality comparison between fresh and frozen/thawed ostrich M. *iliofibularis*. *Meat Science*, *91*, 364–368. doi:10.1016/j.meatsci.2012.02.020

Lindsey, P. A., Roulet, P. A., & Romañach, S. S. (2007). Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation*, *134*, 455–469. doi:10.1016/j.biocon.2006.09.005

Lindsey, P. A., Havemann, C. P., Lines, R. M., Price, A. E., Retief, T. A., Rhebergen, T., … Romañach, S. S. (2013). Benefits of wildlife-based land uses on private lands in Namibia and limitations affecting their development. *Oryx*, *47*, 41–53. doi:10.1017/S0030605311001049

Lomiwes, D., Farouk, M. M., Wu, G., & Young, O. A. (2014). The development of meat tenderness is likely to be compartmentalised by ultimate pH. *Meat Science*, *96*, 646–651. doi:10.1016/j.meatsci.2013.08.022

MacMillan, D. C., & Phillip, S. (2008). Consumptive and non-consumptive values of wild mammals in Britain. *Mammal Review*, *38*, 189–204. doi:10.1111/j.1365-2907.2008.00124.x

Magwedere, K., Sithole, F., Hoffman, L. C., Hemberger, Y. M., & Dziva, F. (2013). Investigating the contributing factors to postmortem pH changes in springbok, eland, red hartebeest and kudu edible offal. *Journal of the South African Veterinary Association*, *84*, E1–7. doi:10.4102/jsava.v84i1.919

Mason, D. R. (1984). Dentition and age determination of the warthog *Phacochoerus aethiopicus* in Zululand, South Africa. *Koedoe*, *27*, 79–119.

Melton, S. L. (1990). Effects of feeds on flavor of red meat: a review. *Journal of Animal Science*, *68*, 4421–4435. doi:/1990.68124421x

Monin, G. (2004). Conversion of muscle to meat: Colour and texture deviations. In W. K. Jensen, D. Carrick, & M. Dikeman (Eds.), *Encyclopedia of Meat Sciences* (pp. 323–330). Oxford, UK: Elsevier Ltd.

Mostert, R., & Hoffman, L. C. (2007). Effect of gender on the meat quality characteristics and chemical composition of kudu (*Tragelaphus strepsiceros*), an African antelope species. *Food Chemistry*, *104*, 565–570. doi:10.1016/j.foodchem.2006.12.006

Mottram, D. S. (1998). Flavour formation in meat and meat products : A review. *Food Chemistry*, *62*, 415–424.

Muriel, E., Ruiz, J., Ventanas, J., & Antequera, T. (2002). Free-range rearing increases (n-3) polyunsaturated fatty acids of neutral and polar lipids in swine muscles. *Food Chemistry*, *78*, 219–225. doi:10.1016/S0308-8146(01)00401-0

Nair, M. N., Suman, S. P., Li, S., Joseph, P., & Beach, C. M. (2014). Lipid oxidation-induced oxidation in emu and ostrich myoglobins. *Meat Science*, *96*, 984–993. doi:10.1016/j.meatsci.2013.08.029

Neethling, J., Hoffman, L. C., & Britz, T. J. (2013). Impact of season on the chemical composition of male and female blesbok (*Damaliscus pygargus phillipsi*) muscles. *Journal of the Science of Food and Agriculture*, *94*, 424–431. doi:10.1002/jsfa.6281

Neethling, J., Hoffman, L. C., & Muller, M. M. (2016). Factors influencing the flavour of game meat: A review. *Meat Science*, *113*, 139–153.

North, M. K., Frylinck, L., & Hoffman, L. C. (2015). The physical and biochemical changes in springbok (*Antidorcas marsupialis*) *Longissimus thoracis et lumborum* and *Biceps femoris* muscle during ageing. *Meat Science*, *110*, 145–152. doi:10.1016/j.meatsci.2015.07.009

North, M. K., Frylinck, L., & Hoffman, L. C. (2016). The changes in springbok (*Antidorcas marsupialis*) *Longissimus thoracis et lumborum* and *Biceps femoris* muscle during the rigour period. *Meat Science*, *110*, 145–152. doi:10.1016/j.meatsci.2015.07.009

North, M. K., & Hoffman, L. C. (2015). Changes in springbok (*Antidorcas marsupialis*) *Longissimus thoracis et lumborum* muscle during conditioning as assessed by a trained sensory panel. *Meat Science*, *108*, 1–8. doi:10.1016/j.meatsci.2015.05.004

Nyafu, K. (2009). *Warthog as an introduced species in the Eastern Cape*. MSc thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

Onyango, C. A., Izumimoto, M., & Kutima, P. M. (1998). Comparison some physical and comparison of some physical and chemical propoerties of selected game meats. *Meat Science*, *49*, 117–125.

Poshiwa, X., Groeneveld, R. A., Heitkönig, I. M. A., & Prins, H. H. T. (2013). Reducing rural households ' annual income fluctuations due to rainfall variation through diversification of wildlife use : portfolio theory in a case study of south eastern Zimbabwe . *Tropical Conservation Science*, *6*, 201–220.

Professional Hunters Association of South Africa (PHASA). (2014). *Revenue from hunting tourists breaks R1 billion mark.* Retrieved from www.phasa.co.za/what-is-in-the-news/phasa-press-release/item/570-revenue-from-hunting-tourists-breaks-r1-billion-mark.html.

Pugliese, C., & Sirtori, F. (2012). Quality of meat and meat products produced from southern European pig breeds. *Meat Science*, *90*, 511–8. doi:10.1016/j.meatsci.2011.09.019

Purslow, P. P. (2005). Intramuscular connective tissue and its role in meat quality. *Meat Science*, *70*, 435–447. doi:10.1016/j.meatsci.2004.06.028

Quaresma, M. A. G., Alves, S. P., Trigo-Rodrigues, I., Pereira-Silva, R., Santos, N., Lemos, J. P. C., … Bessa, R. J. B. (2011). Nutritional evaluation of the lipid fraction of feral wild boar (*Sus scrofa scrofa*) meat. *Meat Science*, *89*, 457–461. doi:10.1016/j.meatsci.2011.05.005

Resano, H., Perez-Cueto, F. J. A., de Barcellos, M. D., Veflen-Olsen, N., Grunert, K. G., & Verbeke, W. (2011). Consumer satisfaction with pork meat and derived products in five European countries. *Appetite*, *56*, 167–70. doi:10.1016/j.appet.2010.10.008

Rincker, P., & Bechtel, P. (2006). Similarities and differences in composition and selected sensory attributes of reindeer, caribou and beef. *Journal of Muscle Foods*, *17*, 65–78. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.1745-4573.2006.00036.x/full

Rødbotten, M., Kubberød, E., Lea, P., & Ueland, Ø. (2004). A sensory map of the meat universe. Sensory profile of meat from 15 species. *Meat Science*, *68*, 137–44. doi:10.1016/j.meatsci.2004.02.016

Sales, J., & Kotrba, R. (2013). Meat from wild boar (*Sus scrofa* L.): A review. *Meat Science*, *94*, 187–201. doi:10.1016/j.meatsci.2013.01.012

Shapiro, S., & Wilk, M. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, *52*, 591–611. Retrieved from http://www.jstor.org/stable/2333709

Spanier, A. M., Vercellotti, J. R., & James, C. (1992). Correlation of sensory, instrumental and chemical attributes of beef as influenced by meat structure and oxygen exclusion. *Journal of Food Science*, *57*, 10–15. doi:10.1111/j.1365-2621.1992.tb05413.x

Swanepoel, M., Leslie, A. J., & Hoffman, L. C. (2014). The influence of season and sex on the carcass yield of common warthog (*Phacochoerus africanus*). *South African Journal of Wildlife Research*, *44*, 179–188.

Taylor, R. G., Labas, R., Smulders, F. J. M., & Wiklund, E. (2002). Ultrastructural changes during aging in M. *Longissimus thoracis* from moose and reindeer. *Meat Science*, *60*, 321–326. doi:10.1016/S0309-1740(01)00120-6

Tichivangana, J. Z., & Morrissey, P. A. (1985). Metmyoglobin and inorganic metals as pro-oxidants in raw and cooked muscle systems. *Meat Science*, *15*, 107–116. doi:10.1016/0309-1740(85)90051-8

Timón, M. L., Carrapiso, A. I., Jurado, A., & van de Lagemaat, J. (2004). A study of the aroma of fried bacon and fried pork loin. *Journal of the Science of Food and Agriculture*, *84*, 825–831. doi:10.1002/jsfa.1740

Tshabalala, P. A., Strydom, P. E., Webb, E. C., & De Kock, H. L. (2003). Meat quality of designated South African indigenous goat and sheep breeds. *Meat Science*, *65*, 563–570. doi:10.1016/S0309-1740(02)00249-8

Valencak, T., & Gamsjäger, L. (2014). Lipids in tissues of wild game : overall excellent fatty acid composition, even better in free- ranging individuals. In P. Paulsen, A. Bauer, & F. J. M. Smulders (Eds.), *Trends in Game Meat Hygiene* (pp. 335–344). Wageningen, Germany: Wageningen Academic Publishers. doi:10.3920/978-90-8686-238-2

Valencak, T. G., Gamsjäger, L., Ohrnberger, S., Culbert, N. J., & Ruf, T. (2015). Healthy n-6/n-3 fatty acid composition from five European game meat species remains after cooking. *BMC Research Notes*, *8*, 273. doi:10.1186/s13104-015-1254-1

Van der Merwe, P., & Saayman, M. (2014). The economic impact of hunting: A regional approach. *South African Journal of Economic and Management Sciences*, *17*, 379–395.

Van der Wal, P. G., Bolink, A. H., & Merkus, G. S. M. (1988). Differences in quality characteristics of normal, PSE and DFD pork. *Meat Science*, *24*, 79–84. doi:10.1016/0309-1740(89)90009-0

Van Schalkwyk, D. L., McMillin, K. W., Witthuhn, R. C., & Hoffman, L. C. (2010). The contribution of wildlife to sustainable natural resource utilization in Namibia: A review. *Sustainability*, *2*, 3479–3499. doi:10.3390/su2113479

Van Schalkwyk, D. L., & Hoffman, L. C. (2010). *Guidelines for the Harvesting of Game for Meat Export*. Windhoek, Namibia: Printech.

Van Zyl, L., & Ferreira, A. V. (2004). Physical and chemical carcass composition of springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus dorcas phillipsi*) and impala (*Aepyceros melampus*). *Small Ruminent Research*, *53*, 103–109. doi:10.1016/j.smallrumres.2003.08.017

Volpelli, L. A., Valusso, R., Morgante, M., Pittia, P., & Piasentier, E. (2003). Meat quality in male fallow deer (*Dama dama*): effects of age and supplementary feeding. *Meat Science*, *65*, 555–562. doi:10.1016/S0309-1740(02)00248-6

Voisey, P. W. (1976). Engineering assessment and critique of instruments used for meat tenderness evaluation. *Journal of Texture Studies, 7*, 11-48

Warris, P. (2000). *Meat Science*. Oxon, USA: CAB Publishing.

White, P. C. L., & Lowe, P. (2008). Wild mammals and the human food chain. *Mammal Review*, *38*, 117–122. doi:10.1111/j.1365-2907.2008.00121.x

Wiklund, E., Dobbie, P., Stuart, A., & Littlejohn, R. P. (2010). Seasonal variation in red deer (*Cervus elaphus*) venison (M. *longissimus dorsi*) drip loss, calpain activity, colour and tenderness. *Meat Science*, *86*, 720–727. doi:10.1016/j.meatsci.2010.06.012

Wong, E., Nixon, L. N., & Johnson, C. B. (1975). Volatile medium chain fatty acids and mutton flavour. *Journal of Agricultural and Food Chemistry*, *23*, 495–498.

Wood, J. D., Enser, M., Fisher, A V, Nute, G. R., Sheard, P. R., Richardson, R. I., … Whittington, F. M. (2008). Fat deposition, fatty acid composition and meat quality: A review. *Meat Science*, *78*, 343–58. doi:10.1016/j.meatsci.2007.07.019

Chapter 8

The characteristics of back bacon produced from the *Longissimus thoracis et lumborum* of common warthog (*Phacochoerus africanus*)

Abstract

The common warthog (*Phacochoerus africanus*) has historically been hunted and consumed by rural communities throughout its distribution range in Africa, while the species currently occurs extra-limitally in parts of South Africa through deliberate introductions. This study aimed to develop a processed product of warthog meat in the form of back bacon (*Longissimus thoracis et lumborum*) as a healthy alternative meat product, and to determine its chemical and sensory characteristics derived from adult and juvenile boars and sows. The highest scored attributes included typical bacon and smoky aroma and flavour, and salty flavour, as well as the textural (mouth-feel) attributes tenderness and juiciness. There was an interaction between sex and age for the fishy aroma ($P = 0.03$), sour/sweaty flavour ($P < 0.01$), and fishy flavour ($P = 0.05$), with all being scored highest in adult males. There were no differences as pertaining to sex and age in bacon's chemical composition were high in protein (~29%) and low in total fat (< 2%). Palmitic (C16:0), stearic (C18:0), linoleic (C18:2ω6), oleic (C18:1ω9c) and arachidonic (C20:4ω6) were the dominant fatty acids. There was an interaction between sex and age for the PUFA:SFA ratio ($P = 0.01$). Despite the differences between sex and age class, the differences are considered negligible regarding the overall profile and healthiness of the bacon.

Keywords: warthog, game meat, *Phacochoerus africanus*, bacon, sensory, flavour, processed products

1 Introduction

The global trend towards healthier and sustainable living promotes the increased production and consumption of the meat from wild animals, also referred to as game meat or venison. Game meat production is promoted as a low-input, high production alternative to traditional animal husbandry (Hoffman & Cawthorn, 2012, Kiley-Worthington, 2014). In general, game animals produce a lean and healthy meat, which is high in protein, low in fat with a favourable fatty acid profile. The low overall lipid content and fatty acid composition is largely attributed to their forage diet and high levels of activity (Valencak & Gamsjager, 2014). Most consumers show a preference for meat and meat products with low amounts of visible fat, and are willing to pay more if they are actually lower in fat as it is associated with increased quality (Girolami, Napolitano, Faraone, Di Bello, & Braghieri, 2014).

Although the formal game meat industry produces sizable quantities game meat in many southern African countries annually (Van Schalkwyk, McMillin, Witthuhn, & Hoffman., 2010, Department of Agriculture, Forestry and Fisheries [DAFF], 2013), it has been suggested that general ignorance regarding the quality aspects of game meat and preparation methods has been crippling the growth of the fresh game meat industry (Chapter 2). According to Bender (1992), meat consumption is primarily influenced by availability, price and tradition. It is also possible that consumers associate game meat with lower quality and flavour attributes and therefore desirability, while they might also be unfamiliar with game meat species (Burger, 2002, Hoffman, Muller, Schutte, Calitz, & Crafford, 2005). However, despite the relative slow growth of the game meat industry, consumers and producers have increasingly become aware of the health attributes of game meat in general and its value as a sustainable red meat source (MacMillan & Phillip, 2008). Game meat is also considered exotic, which is attractive to consumers who are adventurous and to foreign tourists to South Africa who want to consume meat from native animals (Hoffman, Crafford, Muller, & Schutte, 2003, Hoffman et al. 2005, Koster, Hodgen, Venegas, & Copeland, 2010).

The meat from wild animals has been associated with a gamey or livery taste (Rødbotten, Kubberød, Lea, & Ueland, 2004). In addition, game meat and the meat from non-ruminants is typically high in total unsaturated FA (UFA) content and thus more susceptible to lipid oxidation (Faustman, Sun, Mancini, & Suman, 2010), which leads to undesirable aromas and flavours. Developing processed game meat products is a potential strategy to introduce the meat of different game species to the commercial market, as the addition of preservatives and anti-oxidants, together with smoking and curing is used to inhibit and/or mask lipid and protein oxidation, thereby increasing shelf life and colour stability whilst imparting specific flavours (Banon, Costa, Gil, & Garrido, 2003, Gandemer, 2002, Van Schalkwyk, McMillin, Booyse, Witthuhn, & Hoffman, 2011). Consumers also appreciate meat products that resemble traditional products in appearance and eating sensation (Tuorila, Meiselman, Cardello, & Lesher, 1998).

A recent report by the World Health Organization's (WHO) International Agency for Research on Cancer (IARC) stated that the consumption of red meat and processed meat products is associated with the risk of certain types of cancer. The IARC placed processed products in the same category as asbestos, second-hand tobacco smoke and gamma radiation, claiming that consuming >50g of processed meat daily increases the risk of colorectal cancer by 18%. The study recommends reduced intake of red meat and processed products but acknowledged that meat is still a valuable source of high nutritional value (Bouvard et al. 2015). Therefore, future meat product development should aim to meet global health recommendations in terms of low total fat and saturated (SFA) content, with favourable polyunsaturated to saturated fatty acid (PUFA:SFA) and omega 3 to omega 3 (n-6:n-3) ratios and decreased preservative (such as salt) content. Game meat has successfully been used in a variety of processed products with beneficial health benefits. For example, studies found that meat products produced from game meat in comparison with domestic animal meat have lower fat contents and higher nutritional values (Paleari, Moretti, Beretta, Mentasti, & Bersani, 2003, Marino, Albenzio, della Malva, Muscio, & Sevi, 2015). Considering the popularity of game meat products such as biltong in South Africa, and alheira sausages in Portugal, increasing research into game meat processing broadens the scope of wild animal production/consumption and global meat provision.

The common warthog (*Phacochoerus africanus*) has historically been hunted and consumed by rural communities throughout its large distribution range across Africa. Currently the species also occurs extra-limitally in parts of South Africa through deliberate introductions and subsequent range expansion. Warthogs are hunted by agricultural producers for damage reprisal, and by recreational and trophy hunters (Nyafu, 2009, Swanepoel, Leslie, & Hoffman, 2016, Chapter 4). This produces a carcass of which the meat can be used for human consumption, as warthogs have a high dressing percentage, low total intramuscular lipid content, high total protein and moisture content and a favourable fatty acid profile (Hoffman & Sales, 2007, Swanepoel, Leslie, & Hoffman, 2014, Chapter 5 & 6). However, the meat from warthogs sometimes exhibits an undesirable flavour described as “sweat/sour” and “fishy” (Chapter 7). This study aimed to develop a processed product of warthog meat in the form of back bacon (*Longissimus thoracis et lumborum*) as a healthy alternative meat product, and to determine the bacon’s chemical and sensory characteristics.

2 Methods

2.1 Sample collection and preparation

Free-roaming warthogs were culled on the Pongola Game Reserve (27° 22' 09.26" S, 31° 50' 42.16" E) situated in KwaZulu Natal province in South Africa. A total number of 31 warthogs were shot using single shot bolt action rifles (Ethical clearance number: 11LV_HOF02), during the daylight hours in March 2015 when sighted, with bias towards sex and age until the desired quota per group (N = 8) was achieved. Unfortunately, only seven warthogs for the group of juvenile males were culled as the full quota could not be obtained within the given time period (Chapter 7). Although other studies used tusk protrusion and molar eruption as the basis for classifying age classes (Mason, 1984), the data capturing team had difficulty in judging their age in the field during culling as warthogs have a secretive and avoidance behaviour towards humans/vehicles (Chapter 6), animals were shot as they were observed with a certain bias towards sex and age, as it was not desired to cull animals unnecessarily (Chapter 7). Therefore, tusk protrusion and estimated body weight was used as a visual tool to determine age classing. In support of this decision, the animals weighing less than 35 kg, with no tusk protrusion past the flanges of the lips were classified as juveniles, and all other animals classified as mature adults.

Immediately after shooting, the animals were exsanguinated by thoracic sticking, transported to a slaughter facility and weighed and dressed according to the *Guidelines for the Harvesting of Game Meat Export* (Van Schalkwyk & Hoffman, 2010). The body weight of the animal was defined as the total weight of the animal (minus the blood lost during exsanguination). Dressing entailed the removal of the head, feet and skin. The head was removed by making a horizontal cut between the axis and atlas bones of the neck vertebrae. The trotters were removed by making a horizontal cut through the metacarpal carpal joint (joints between the carpal joints and radius and ulna). The skin was removed by starting at the anus and working towards the neck area, while attempting to leave as much subcutaneous fat on the carcass as possible. After evisceration the carcass was washed, allowed to drip dry for ± 20 minutes before being weighed again to determine hot carcass weight. After the carcass was stored at 4ºC it was weighed again to determine cold carcass weight (24h post mortem). The *Longissimus thoracis et lumborum* (LTL) muscles excised from the carcass were weighed, vacuum packed and frozen at –20ºC before being transported to Stellenbosch University. The right LL was used for bacon production and subsequent sensory and chemical analyses.

2.2 pH

A pH measurement was taken from the LTL muscle (~ 3rd last rib) ± 45 min after exsanguination using a Crison pH25 handheld portable pH meter (Lasec (Pty) Ltd, South Africa). Before each reading, the meter was calibrated with standard buffers (pH 4.0 and pH 7.0) as provided by the manufacturer. A final measurement was at taken 24 hours after they were excised and considered as ultimate pH (pH_u).

2.3 Bacon production

The recipe and spices for the bacon was sourced from a commercial producer, Deli Spices™ (Ready Brine for 10 ℓ Water 1.5 Kg Ref: 01124015, 25 Bertie Avenue, Epping 2, Cape Town, South Africa) (Table 1). The LTL muscles were thawed overnight (12h) at 4°C. The thawed muscles were dabbed dry with a paper towel and weighed to determine thaw loss. It was initially envisaged to produce back bacon following commercial processing methods (i.e. by injection) to achieve a pick up of 20%, but since the muscles differed in size between ages it was decided to submerge the muscles in a brine solution for ± 72 hrs, at fridge temperatures of 3.9°C (± standard deviation [SD] 0.37). After brining, the LTL were smoked in a commercial smoker Reich Airmaster® UKF 2000 BE (Reich Klima-Räuchertechnik, Urbach, Germany) with a SmartSmoker and TradiSmoker LS 500 HP electronic, automatically controlled by a Microprocessor (Unicontrol 2000), according to the program as set out in Table 2. The relative humidity was controlled by the chamber. A thermocouple probe was inserted to one bacon sample to measure the change in core temperature during the smoking program, while the chamber provided the measurements of chamber temperature and relative chamber humidity. The changes are illustrated in Figure 1. After smoking, the LTL were weighed again to determine final weight change, vacuum packed and frozen at -20°C until further analysis.

Table 20: Ingredients of the brine used (Deli Spices™).

Component	Ingredients
Seasoning	Emulsifiers (E451, E452, E339), Dextrose, Sugar, Maltodextrin, Sodium Erythorbate (E316), Acidity regulator (Citric Acid [E330])
	Salt, Ascorbic acid (E300), Anticaking agent (Silicon Dioxide [E551])
Curing salt*	Salt, Sodium Nitrite [E250], Sodium Nitrate [E251]), Colourant (C.I.45430).
Salt	NaCl

*Flavourings are natural and nature identical.

Table 21: The smoking program of the Reich Airmaster® as used for preparing warthog *Longissimus thoracis et lumborum* (back) bacon.

Smoking program	Temperature (°C)	Relative humidity	Time (min)
Reddening	45	0	15
Drying	45	0	15
Hot smoke	45	0	20
Smoke destruction	45	0	10
Hot smoke	45	0	25
Smoke destruction	55	0	10
Drying	45	0	10

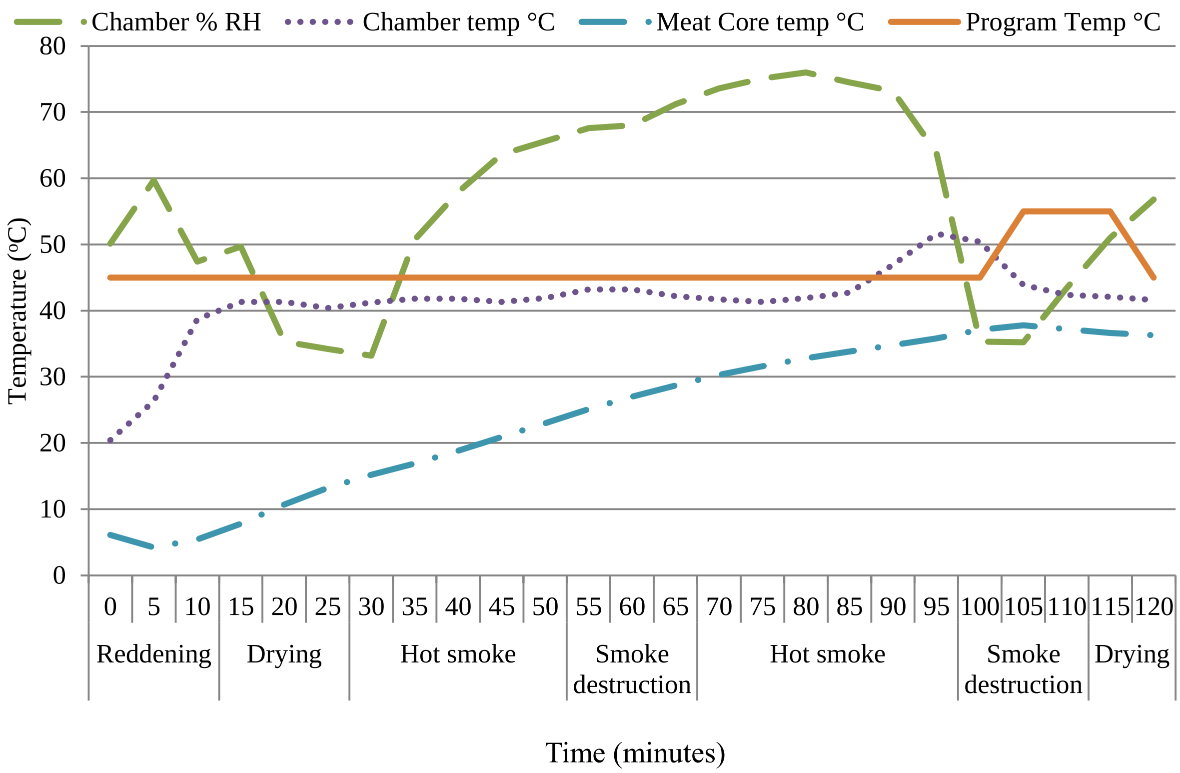

Figure 19: The temperature (°C) and relative humidity of the smoking program and temperature (°C) of the chamber and core of *Longissimus thoracis et lumborum* (back) bacon.

2.4 Descriptive sensory analysis

The entire LTL bacon was divided to roughly represent the *Longissimus thoracis* (LT) (T_3 to T_{12}/T_{13}) and *Longissimus lumborum* (LL) (T_{12}/T_{13} to L_5) portion, with the separate portions being weighed again.

The visible fat and tendons were removed before the LT portion was homogenized, vacuum packed and stored at –20ºC for chemical analysis. The LL portion was vacuum packed and stored at 4ºC prior to sensory analysis the subsequent day. The LL portion for sensory analysis was removed from vacuum package, gently blotted dry with a paper towel and the whole (i.e not sliced) LL was placed in individually marked oven bags (Glad®), and prepared according to the method described by Geldenhuys, Hoffman, and Muller (2014). After cooking the LL was removed from bags and allowed to cool for 10 minutes before being weighed to determine cooking loss, and subsequently cut into 1.2 cm^3 cubes. The cubes were wrapped in aluminium foil and placed in ramekins and reheated at 100ºC for 7 minutes. After preheating the meat was covered with petri-dish lids and placed on half-filled cups in waterbaths heated to 70ºC in order to maintain temperature.

A panel of 10 judges were trained according to Lawless and Heymann (2010) using generic descriptive techniques. The panellists were recruited from a pre-existing group of judges involved with research studies on meat at Stellenbosch University. During six one hour long training sessions the panellists made use of reference samples to formulate a list of sensory attributes, including aroma, flavour and texture. The sensory attributes and reference samples are described in Table 2. The cooked bacon samples were evaluated by the trained panellists during seven blind-tasting sessions of ± 45 minutes that scored each attribute on an unstructured 100-point scale. The cooked samples were presented to, and the data collected from, panellists using Compusense® five software (Compusense, Guelph, Canada) whilst seated in booths in a temperature (21ºC) and light (artificial daylight) controlled room. Each panellist received three samples of warthog bacon randomly assigned to the session per treatment. The test reproducibility of the trained panel was determined using test-retest as described by Geldenhuys et al. (2014).

Table 22: Definition and scale of each attribute used for the descriptive sensory analysis of warthog back bacon.

Sensory attribute	Description	Reference
Aroma*		
Typical bacon aroma	Associated with typical bacon	Back bacon
Smoky aroma	Associated with smoked meat products	Liquid smoke solution
Sweet aroma	Associated with pork loins chops	Pork loin chop
Gamey aroma	Associated with game meat	Fallow deer loin
Fishy aroma	Associated with smoked mackerel	Smoked mackerel
Sour/sweaty aroma	Associated with warthog meat	Warthog fillet
Flavour*		
Typical bacon flavour	Associated with typical bacon	Back bacon
Smoky flavour	Associated with smoked meat products	Back bacon
Salty flavour	Associated with typical bacon	Salt solution
Sweet flavour	Associated with pork loins chops	Sugar solution
Gamey flavour	Associated with game meat	Fallow deer loin
Sour/sweaty flavour	Associated with warthog meat	Warthog fillets
Fishy flavour	Associated with smoked mackerel	Smoked mackerel
Texture (mouth-feel)		
Initial juiciness	Amount of fluid exuded when pressed between thumb and forefinger (0 = Dry, 100 = Juicy)	Chicken breast
Tenderness	Impression formed after first 5 chews using molar teeth (0 = Dry, 100 = Juicy)	Chicken breast
Sustained juiciness	Impression formed after first 5 chews using molar teeth (0 = Tough, 100 = Tender)	Chicken breast
Residue	Amount of residue left in mouth after 10 chews using molar teeth (0 = None, 100 = Abundant)	Pork loin chops**
Appearance		
Appearance of muscle fibre bundles	Appearance of muscle fibres 0 = Fine, 100 = Coarse	Chicken breast

*Scale for descriptors: 0 = Low, 100 = High, unless otherwise stated. Aroma and flavour were analysed orthonasally and retronasally, respectively.
**Cooked to internal temperature of 75°C.

2.5 Proximate analyses

The total moisture, ash and crude protein content (%) was determined on the back bacon according to the Association of Official Analytical Chemist's Standard Techniques (AOAC) method 934.01 (for moisture content), method 942.05 (for ash content) and the Dumas combustion method 992.15 (for crude protein content) (AOAC 1992, 2002a, 2002b). Total moisture content was determined using a 2.5 g homogenized sample. The moisture-free sample was used to determine total ash content. A 0.15 g, defatted, dried and finely ground sample was used for crude protein analysis with a Leco Nitrogen/Protein Analyser (FP – 528, Leco Corporation). Before the analyses the machine was calibrated using 0.15 g ethylenediamineteraacetic acid (EDTA) samples (Leco Corporation, 3000 Lakeview Avenue, St. Joseph, MI 49085-2396, USA, Part no.502-092, Lot no. 1055). After 20-30 analyses the machine was again calibrated with EDTA samples. The percentage Nitrogen (% N) per sample was determined and multiplied by a conversion factor of 6.25 to calculate the total crude protein content per sample. The chloroform/methanol (1:2, vol/vol) extraction method as described by Lee, Trevino, and Chaiyawat (1996) was used to determine the total lipid content using a 5 g sample. The laboratory at the Department of Animal Sciences, Stellenbosch University, is accredited by the Agricultural Laboratory Association of South Africa (AgriLASA) to perform accurate and reliable proximate analyses and for validation of accuracy and repeatability, partakes in monthly inter-laboratory blind tests.

2.6 Shear force

The Warner Bratzler shear force (WBSF) test was used to determine the instrumental shear force of the cooked back bacon samples as described by Honikel (1998). The samples were wrapped in aluminium foil, placed in plastic bags and refrigerated at 4^{o}C for three days (72 hrs) before being subjected to analyses. Three adjacent 1 cm x 1 cm meat strips were cut parallel to the muscle fibre direction, and cut further into a minimum of six rectangular cubes (1x1x2 cm). An Instron Universal Testing Machine attached with a WBSF fitting (Voisey, 1976) was used to determine the shear force required to cut the meat sample perpendicularly to the muscle fibres at a crosshead speed of 200 mm/min. Shear values were recorded in Newton (N) and an average was calculated according to the number of samples.

2.7 Fatty acid analysis

The fatty acids were extracted according to the method described by Folch, Lees, and Sloane-Stanley (1957). Chloroform/methanol (1:2, vol/vol) solution was used for extraction of a 2 g homogenized sample. The extraction solution contained 0.01 % butylated hydroxytolene (BHT) to act as an anti-oxidant. A 2 g meat sample and 20 ml solution was homogenized using a polytron mixer (Kinematica, type PT 10–35, Switzerland). Heptadecanoic acid (C17:0) was added (0.5 ml) to the homogenized sample as an internal standard in order to quantify the observed fatty acids in the sample (Internal standard: Catalogue number H3500, Sigma-Aldrich Inc., 3050 Spruce Street, St. Louis, MO 63103, USA). A 250 µL sub-sample of the extraction was transmethylated for 2 h at 70°C in a water-bath using methanol/sulphuric acid (19:1, vol/vol) as transmethylating agent (2 ml). The transmethylated sample was cooled to room temperature before the fatty acid methyl esters (FAME) were extracted by adding 1 ml dH2O and 2 ml hexane to the sample and transferring the top hexane layer. The sample was dried under nitrogen, after which 50 µL hexane was added, of which 1 µL was injected into the gas chromatograph. The FAMEs were analysed using a Thermo TRACE 1300 series gas-chromatograph (Thermo Electron Corporation, Milan, Italy) equipped with a flame-ionisation detector, using a 30 m TR-FAME capillary column with an internal diameter of 0.25 mm and a 0.25 µm film (Cat. No. HY260M142P, Anatech, Cape Town, South Africa) and a run time of *ca*. 40 mins. The following oven temperature settings were utilised: initial temperature of 50 °C (maintained for 1 min) and final temperature of 240 °C attained after three ramps (initial increase at a rate of 25 °C/min until a temperature of 175 °C was reached; thereafter an immediate increase at a rate of 1.5 °C/min to reach 200 °C and maintenance of this temperature for 6 min; lastly an increase at a rate of 10 °C/min to reach 240 °C and maintenance of this temperature for a minimum of 2 min). The injector temperature was set at 240 °C and the detector temperature at 250 °C. The hydrogen gas flow rate was 40 mL/min. The FAME of each sample was identified by comparing the retention times with those of a standard FAME mixture (Supelco™ 37 Component FAME mix, Cat no. 47885-U, Supelco, USA), with results being expressed as mg fatty acid/g meat. Results were given as a milligram per gram of fatty acids present in bacon.

2.8 Statistical analysis

The study design consisted of four treatments with age and sex as the main factors. Seven warthogs were randomly assigned to each testing session, resulting in seven replications per treatment. The sensory data was pre-analysed using the software program Panelcheck (Version 1.3.2, www.panelcheck.com) to evaluate the consistency of the sensory panel. The physical and chemical data was analysed by Analysis of variance (ANOVA) using SAS software (Statistical Analysis Software 2006, Version 9.2, SAS Institute Inc., Cary, NC, USA). The sensory data was analysed by test-retest Analysis of variance (ANOVA) using SAS software to determine the reliability of the data. The normality of the data as analysed using the Shapiro-Wilk test (Shapiro & Wilk, 1965), and outliers were identified from normal probability plots, and removed where deemed necessary. Analysis of variance was performed on all the data using the GLM (General Linear Model) procedure. The model for the experimental design is indicated by the following equation:

$$y_{ijk} = \mu + s_j + a_k + sa_{ik} + \varepsilon_{ijk}$$

The terms within the model are defined as: the response obtained for the i^{th} observation for the j^{th} gender (y_{ijk}), the overall mean (μ), the sex main effect (s_j), the age main effect (a_k), the sex by age interaction effect (sa_{ij}) and the random error (ε_{ijk}) associated with response on the i^{th} observation in the j^{th} sex and the k^{th} age. For post hoc testing, Fisher's LSD was used when the main effects/interactions analysed were significant. A 5% level of significance was used as a guideline to explain significantly differences. Pearson's correlation was used to determine the correlation coefficients for the sensory, physical and chemical data. Principal component analyses (PCA) and discriminate analysis (DA) were performed using the correlation matrix to determine and illustrate relationships between the sensory, physical and chemical data.

3 Results

The physical measurements of the culled warthogs and chemical composition of the cooked back bacon is presented in Table 4. There were no interactions between sex and age for the physical and chemical measurements. The dead and carcass weight of warthogs differed between sexes ($P = 0.02$ and $P = 0.05$, respectively) and ages ($P < 0.001$ and $P < 0.001$, respectively), where the adult boars were heavier than the adult sows and the adults heavier than the young warthogs, the latter did not differ between sexes, while the LTL muscle from adults were heavier ($P < 0.001$) than that of the juvenile warthogs. There was no sex or age effect on the thawing and cooking losses, while the final pick up % was the highest in juvenile females compared to males ($P < 0.01$), but the others did not differ from each other. The total weight change % was highest for female adults compared to juvenile males ($P = 0.03$), which also did not differ among the others. Ash content was higher in adults compared to juveniles, with the male juveniles significantly differing from adults ($P = 0.03$). None of the other chemical characteristics of the cooked back bacon differed among the four groups, and were high in protein (~29%) and low in total fat (< 2%) contents. Cooking loss was negatively correlated with moisture %, (-0.64, $P < 0.01$) and positively with protein (0.55, $P < 0.01$) and fat (0.44, $P = 0.01$), whilst pick up % was positively correlated with ash content ($r = 0.46$, $P = 0.01$). Moisture content was negatively correlated with protein content ($r = -0.91$, $P = < 0.01$).

Table 23: The average values (± SD) of the physical measurements of warthog carcasses and chemical composition of cooked back bacon according to sex and age.

Component	Adult females (n = 8)	Adult males (n = 8)	Juvenile females (n = 8)	Juvenile males (n = 7)
Body weight (kg)	$52.83^{b} \pm 7.80$	$63.56^{a} \pm 9.94$	$33.01^{c} \pm 4.96$	$37.40^{c} \pm 11.72$
Hot carcass weight (kg)	$26.78^{b} \pm 3.49$	$32.65^{a} \pm 6.50$	$17.41^{c} \pm 4.12$	$17.97^{c} \pm 6.25$
Cold carcass weight (kg)	$26.13^{b} \pm 3.43$	$31.81^{a} \pm 6.44$	$16.19^{c} \pm 2.89$	$17.49^{c} \pm 6.16$
Dress out (%)*	$49.6^{a} \pm 1.67$	$49.8^{a} \pm 2.88$	$49.0^{a} \pm 2.63$	$46.4^{b} \pm 3.26$
LTL weight (kg)	$0.87^{a} \pm 0.13$	$1.03^{a} \pm 0.24$	$0.63^{b} \pm 0.12$	$0.62^{b} \pm 0.16$
pH_{45}	6.21 ± 0.37	6.33 ± 0.23	6.29 ± 0.27	6.15 ± 0.20
pH_{24}	5.63 ± 0.01	5.55 ± 0.07	5.58 ± 0.07	5.63 ± 0.09
Thaw loss# (%)	11.87 ± 2.59	11.80 ± 3.32	11.66 ± 2.47	11.48 ± 2.35
Final pick up# (%)	$14.06^{ab} \pm 1.07$	$13.32^{b} \pm 1.61$	$14.70^{a} \pm 1.00$	$14.43^{ab} \pm 1.48$
Smoking loss# (%)	7.91 ± 1.34	7.74 ± 1.27	9.13 ± 1.75	8.96 ± 2.42
Total weight change# (%)	$2.99^{a} \pm 1.54$	$2.53^{ab} \pm 1.06$	$1.51^{ab} \pm 1.63$	$1.19^{b} \pm 2.46$
Cooking loss# (%)	11.31 ± 5.51	12.74 ± 5.40	12.24 ± 4.53	11.79 ± 4.16
Shear force# (N)	28.11 ± 6.90	27.02 ± 6.03	26.83 ± 2.29	25.97 ± 5.36
Moisture# (%)	67.67 ± 2.83	67.54 ± 1.30	67.02 ± 1.62	66.57 ± 1.58
Protein# (%)	29.36 ± 2.65	29.19 ± 1.25	29.59 ± 1.53	29.85 ± 1.61
Fat# (%)	1.40 ± 0.60	1.25 ± 0.50	1.27 ± 0.42	1.27 ± 0.39
Ash# (%)	$5.47^{b} \pm 0.75$	$5.29^{b} \pm 0.58$	$5.74^{ab} \pm 0.98$	$6.25^{a} \pm 0.43$

$^{a-c}$Least square means in the same row with different superscripts are significantly different ($P < 0.05$).
*Calculated using cold carcass weight.
#Determined for *LL* back bacon.

The mean scores for the descriptive sensory attributes are presented in Table 5. During training, attribute descriptors used to describe the aroma and flavour pertaining to boar taint in domestic boars were considered by the panel as aroma and flavour descriptors, but not included in the final analysis as these were not detected by the panellists. The undesirable odour and flavoured described as "sour/sweaty" and "fishy" were scored low and there was a significant interaction between sex and age for the fishy aroma ($P = 0.03$), sour/sweaty flavour ($P < 0.01$), and fishy flavour ($P = 0.05$), with all being scored highest in adult males. The residue of the bacon from adult males was higher compared to juvenile females ($P = 0.04$), while the muscle fibres of the bacon from adult females appeared coarser compared to juvenile males ($P = 0.03$), but these attributes did not differ for the others. The other attributes did not differ according to sex or age ($P > 0.05$), with the highest scored attributes including typical bacon and smoky aroma and flavour, and salty flavour, as well as the textural (mouth-feel) attributes tenderness and juiciness.

Table 24: The mean values (± SD) of the sensory attributes of cooked warthog back bacon according to sex and age.

Sensory attribute	Adult female (n = 7)	Adult male (n = 7)	Juvenile female (n = 7)	Juvenile male (n = 7)
Typical bacon aroma	72.35 ± 1.98	72.81 ± 0.82	72.19 ± 1.46	72.64 ± 1.00
Smoky aroma	71.93 ± 1.27	71.41 ± 1.46	72.18 ± 1.36	72.37 ± 1.66
Sweet aroma	9.17 ± 0.62	9.17 ± 0.84	9.76 ± 0.35	9.29 ± 0.54
Fishy aroma	$1.20^{b} \pm 0.12$	$1.48^{a} \pm 0.24$	$1.24^{b} \pm 0.14$	$1.23^{b} \pm 0.12$
Sour/sweaty aroma	0.36 ± 0.61	0.60 ± 0.60	0.34 ± 0.58	0.16 ± 0.42
Typical bacon flavour	72.38 ± 0.56	72.33 ± 0.81	72.53 ± 0.35	72.94 ± 0.95
Smoky flavour	73.64 ± 0.93	73.13 ± 1.36	72.14 ± 2.37	73.31 ± 1.21
Salty flavour	38.60 ± 2.69	39.55 ± 1.93	39.90 ± 2.40	40.37 ± 1.68
Sweet flavour	4.37 ± 0.93	4.14 ± 1.05	4.52 ± 0.59	3.88 ± 1.47
Sour/sweaty flavour	0	0.72 ± 0.68	0	0
Fishy flavour	3.42 ± 1.02	4.08 ± 0.86	3.93 ± 1.41	2.98 ± 0.73
Initial juiciness	54.28 ± 1.82	54.37 ± 2.59	53.71 ± 2.69	53.61 ± 2.91
Tenderness	67.85 ± 3.08	67.66 ± 1.98	68.39 ± 2.09	68.78 ± 1.67
Sustained juiciness	66.47 ± 1.55	68.11 ± 2.56	67.64 ± 1.64	68.28 ± 1.27
Residue	$22.74^{ab} \pm 1.59$	$23.78^{a} \pm 0.76$	$22.05^{b} \pm 1.05$	$22.55^{ab} \pm 1.11$
Appearance of muscle fibre bundles	$32.56^{a} \pm 2.64$	$31.29^{ab} \pm 2.15$	$30.42^{ab} \pm 1.78$	$29.33^{b} \pm 2.79$

$^{a\text{-}b}$Least square means in the same row with different superscripts are significantly different ($P < 0.05$).

The fatty acid (FA) composition of the four groups is presented in Table 6. There was significant interaction between sex and age for the polyunsaturated to saturated (PUFA:SFA) ratio (*P* = 0.01), with the ratio highest for juvenile males compared to adult males and juvenile females but not adult females. The other fatty acids were similar (*P* > 0.05). SFA and PUFA contributed primarily to the FA composition, with palmitic (C16:0), stearic (C18:0), linoleic (C18:2ω6), oleic (C18:1ω9c) and arachidonic (C20:4ω6) being the dominant FA. A princinple component analysis (PCA) bi-plot (Figure 2) shows the sensory profile for each animal according to physical attributes, approximate composition and FA composition, with Factor 1 explaining 34.59% of the variance. A complete correlation matrix is given in Table 7 to show the significant correlations between sensory attributes and approximate and FA composition. Total pick up % was positively correlated with muscle weight (r = 0.45, *P* < 0.01) and salty flavour (r = 0.60, *P* < 0.01), and shear force was negatively correlated with tenderness (r = -0.60, *P* < 0.01). The panel did not detect any gamey aroma or flavour between the treatments, and therefore no results/correlations are available.

Table 25: The average mg·g^{-1} (± SD) of the fatty acid composition of cooked warthog back bacon according to age and sex.

Fatty acid	Adult females	Adult males	Juvenile females	Juvenile males
Saturated fatty acids				
C12:0	0.05 ± 0.01	0.04 ± 0.02	0.04 ± 0.03	0.03 ± 0.03
C13:0	0.09± 0.04	0.07 ± 0.07	0.05 ± 0.05	0.10 ± 0.04
C14:0	0.07 ± 0.02	0.07 ± 0.04	0.08 ± 0.05	0.07 ± 0.04
C15:0	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01	0.01 ± 0.01
C16:0	2.61 ± 1.01	2.70 ± 1.20	2.78 ± 1.20	2.20 ± 0.81
C18:0	1.66 ± 0.64	1.79 ± 0.66	1.86 ± 0.87	1.45 ± 0.47
C20:0	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.01 ± 0.001
C21:0	0.18 ± 0.07	0.17 ± 0.06	0.16 ± 0.05	0.17 ± 0.07
C22:0	0.01 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.01 ± 0.004
C23:0	0.22 ± 0.10	0.23 ± 0.08	0.21 ± 0.01	0.21 ± 0.09
Monounsaturated fatty acids				
C14:1	0.03 ± 0.01	0.03 ± 0.01	0.03 ± 0.01	0.03 ± 0.01
C16:1	0.15 ± 0.06	0.12 ± 0.05	0.12 ± 0.04	0.11 ± 0.05
C18:1ω9c	1.64 ± 0.88	1.23 ± 0.83	1.21 ± 0.62	1.43 ± 0.69
Polyunsaturated fatty acids				
C18:2ω6c	3.82 ± 1.99	2.91 ± 1.47	2.96 ± 0.88	3.53 ± 1.03
C18:3ω3	0.48 ± 0.20	0.43 ± 0.20	0.43 ± 0.20	0.44 ± 0.22
C20:2ω6	0.04 ± 0.02	0.03 ± 0.01	0.03 ± 0.02	0.03 ± 0.01
C20:3ω6	0.38 ± 0.15	0.33 ± 0.12	0.31 ± 0.08	0.34 ± 0.12
C20:3ω3	0.26 ± 0.12	0.26 ± 0.09	0.25 ± 0.09	0.30 ± 0.10
C20:4ω6	1.27 ± 0.49	1.02 ± 0.50	1.03 ± 0.28	1.17 ± 0.42
C20:5ω3	0.38 ± 0.20	0.38 ± 0.16	0.41 ± 0.12	0.51 ± 0.19
C22:6ω3	0.27 ± 0.16	0.22 ± 0.09	0.22 ± 0.06	0.24 ± 0.09
SFA	4.93 ± 1.89	5.11 ± 2.02	5.31 ± 2.20	4.29 ± 1.40
MUFA	1.81 ± 0.94	1.36 ± 0.88	1.70 ± 0.91	1.57 ± 0.74
PUFA	7.28 ± 3.72	5.73 ± 2.59	5.77 ± 1.53	6.85 ± 1.97
PUFA:SFA	1.46^{ab} ± 0.31	1.18^{b} ± 0.45	1.20^{b} ± 0.36	1.62^{a} ± 0.12
ω6:ω3	3.98^{a} ± 0.92	3.13^{b} ± 0.64	3.14^{b} ± 0.71	3.01^{b} ± 0.71

[a-b]Least square means in the same row with different superscripts are significantly different ($P < 0.05$).

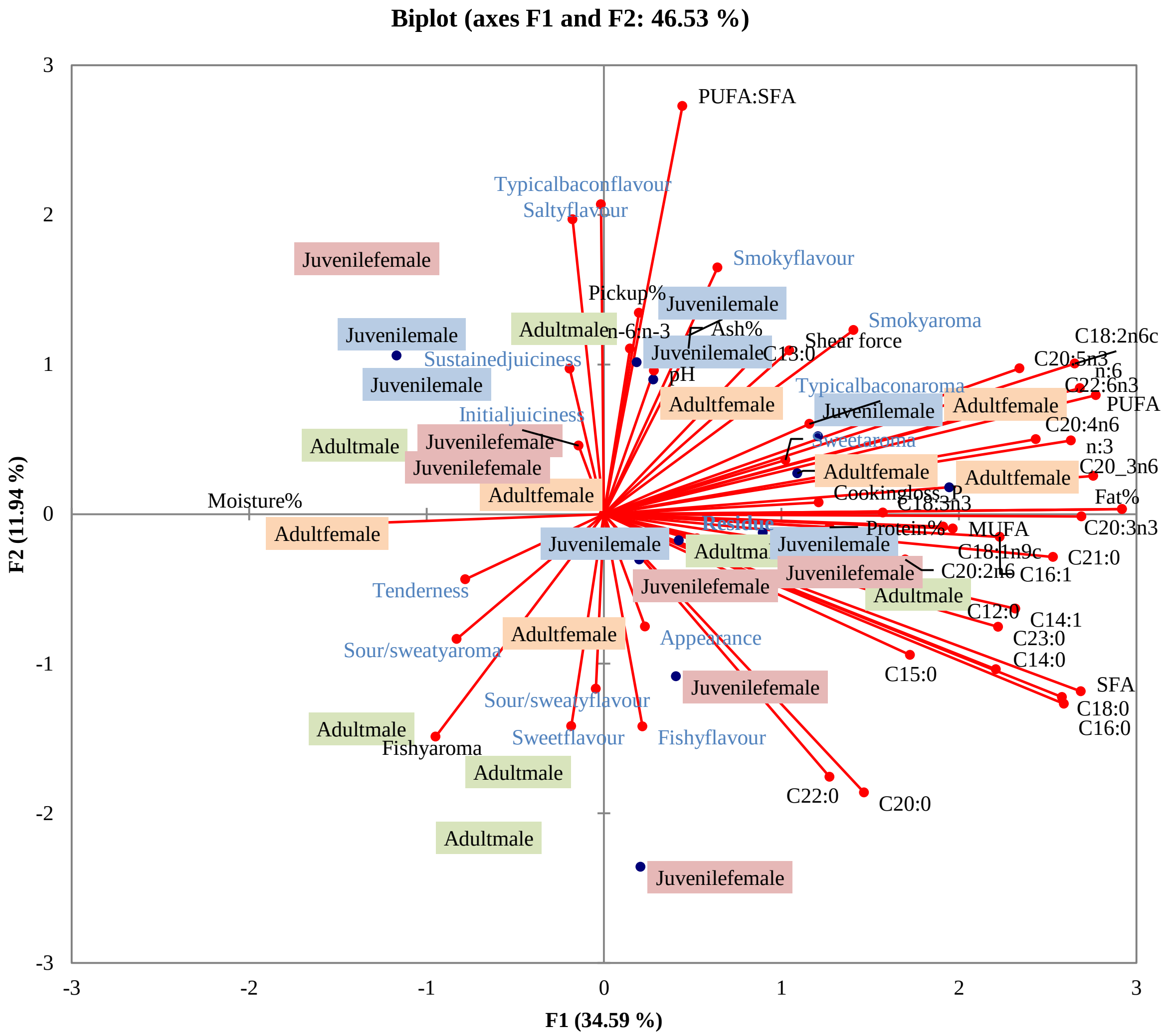

Figure 1: The PCA bi-plot of sensory attributes, physical attributes, proximate composition and fatty acid composition of warthog back bacon according to sex and age.

Table 26: Correlation matrix between the sensory attributes, proximate composition and fatty acid composition of warthog back bacon.

Variables*	Typical bacon aroma	Smoky aroma	Sweet aroma	Fishy aroma	Sour/ sweaty aroma	Appearance	Initial juiciness	Typical bacon flavour	Smoky flavour	Salty flavour	Sweet flavour	Sour/ sweaty flavour	Fishy flavour	Tenderness	Sustained juiciness	Residue
C12:0	0.221	0.209	0.357	-0.140	-0.193	-0.062	-0.066	-0.152	0.023	-0.209	-0.158	-0.048	0.005	-0.007	0.133	-0.091
C13:0	-0.070	0.122	0.300	-0.129	0.120	0.082	0.224	0.100	-0.026	0.241	-0.221	-0.252	-0.191	0.134	0.163	0.050
C14:0	0.042	0.175	0.290	-0.152	-0.232	-0.048	-0.331	-0.247	-0.001	-0.165	0.165	-0.029	0.259	-0.077	-0.201	0.079
C15:0	0.220	0.242	0.285	-0.311	-0.144	-0.018	-0.263	-0.206	-0.080	-0.228	0.073	0.060	0.127	-0.016	-0.114	-0.047
C16:0	0.251	0.229	0.235	-0.182	-0.169	0.186	-0.157	-0.289	-0.064	-0.308	0.233	0.113	0.187	-0.178	-0.254	0.176
C18:0	0.276	0.222	0.238	-0.077	-0.119	0.097	-0.103	-0.194	0.007	-0.260	0.196	0.126	0.263	-0.222	-0.240	0.250
C20:0	-0.003	-0.048	0.246	0.155	0.165	0.025	0.075	-0.261	-0.300	-0.284	0.128	0.143	0.220	-0.087	-0.217	0.049
C21:0	0.324	0.353	0.218	-0.122	-0.149	0.027	0.060	0.000	0.135	-0.168	-0.127	0.056	0.017	-0.254	0.080	0.066
C22:0	-0.038	0.020	0.091	0.277	0.175	0.136	0.015	-0.271	-0.303	-0.307	0.130	0.109	**0.405**	-0.030	-0.198	0.050
C23:0	0.322	0.308	0.169	-0.020	-0.079	0.015	0.050	-0.069	0.056	-0.248	-0.104	0.135	0.046	-0.247	0.010	0.005
C14:1	0.334	0.341	0.272	-0.054	-0.123	-0.029	0.004	-0.011	0.114	-0.173	-0.133	0.122	0.058	-0.306	0.011	0.015
C16:1	0.066	0.160	0.162	-0.275	-0.176	0.172	-0.068	-0.191	0.093	-0.142	0.167	-0.102	0.143	-0.218	-0.124	0.261
C18:1ω9c	0.149	0.247	0.174	-0.184	-0.232	0.200	-0.140	-0.164	0.128	0.042	0.180	0.030	0.205	-0.149	-0.319	0.336
C18:2ω6c	0.309	**0.470**	0.245	**-0.422**	-0.294	0.052	0.013	0.157	0.329	0.110	-0.101	-0.095	-0.068	-0.248	0.043	0.260
C18:3ω3	0.191	0.356	0.245	-0.139	-0.186	0.014	-0.277	-0.150	0.112	0.071	-0.019	-0.013	0.147	0.095	-0.233	-0.009
C20:2ω6	0.359	0.347	-0.047	-0.098	0.146	0.188	0.026	0.122	0.355	-0.309	-0.159	0.089	-0.090	-0.162	-0.099	0.149
C20:3ω6	**0389**	**0.409**	0.227	-0.295	-0.228	0.073	0.066	0.091	0.230	-0.070	-0.108	-0.023	-0.061	-0.272	0.086	0.163
C20:3ω3	**0.460**	**0.566**	0.306	-0.190	-0.233	-0.028	-0.094	0.044	0.256	-0.066	-0.188	0.022	0.011	-0.156	-0.032	0.048
C20:4ω6	0.197	0.275	0.047	**-0.379**	-0.286	0.177	0.020	0.059	0.208	-0.043	0.088	-0.018	-0.133	-0.320	0.054	0.289
C20:5ω3	0.387	0.453	0.349	-0.336	-0.246	-0.104	0.141	0.256	0.277	0.106	-0.333	-0.146	-0.131	-0.139	0.277	0.045
C22:6ω3	0.366	**0.402**	0.268	-0.338	-0.255	-0.037	0.090	0.215	0.277	0.153	-0.291	-0.071	-0.099	-0.222	0.195	0.113
SFA	0.267	0.248	0.259	-0.145	-0.147	0.142	-0.116	-0.238	-0.029	-0.280	0.179	0.104	0.198	-0.195	-0.217	0.190
MUFA	0.149	0.247	0.177	-0.191	-0.231	0.199	-0.136	-0.166	0.128	0.030	0.179	0.024	0.204	-0.157	-0.310	0.334
PUFA	0.325	**0.466**	0.239	**-0.403**	-0.303	0.066	-0.011	0.116	0.300	0.068	-0.088	-0.073	-0.066	-0.238	0.037	0.228

PUFA:SFA	0.175	**0.410**	0.092	**-0.481**	-0.311	-0.158	0.085	**0.502**	**0.436**	**0.492**	**-0.394**	-0.319	-0.399	-0.121	0.303	0.021
ω6	0.292	**0.425**	0.193	**-0.415**	-0.295	0.093	0.019	0.130	0.300	0.056	-0.050	-0.071	-0.089	-0.278	0.049	0.271
ω3	**0.387**	**0.533**	0.366	-0.292	-0.280	-0.040	-0.114	0.046	0.254	0.098	-0.210	-0.070	0.026	-0.055	-0.012	0.038
ω6: ω3	-0.180	-0.100	-0.218	-0.333	0.001	0.150	0.226	0.209	0.069	0.060	0.148	-0.132	-0.198	-0.361	0.132	0.323
Moisture %	-0.105	-0.084	-0.237	0.260	0.251	-0.021	-0.107	-0.065	0.083	-0.108	0.132	0.063	-0.244	0.062	-0.232	0.005
Protein %	0.068	0.016	0.205	-0.198	-0.179	0.103	0.166	0.015	-0.153	0.017	-0.081	-0.114	0.210	-0.071	0.274	-0.046
Fat %	0.310	**0.404**	0.263	-0.321	-0.271	0.126	-0.073	-0.047	0.189	-0.052	0.045	-0.002	0.069	-0.236	-0.113	0.262
Ash %	-0.116	0.036	-0.082	-0.288	-0.373	-0.353	0.058	0.242	0.108	**0.422**	-0.270	-0.115	-0.057	0.030	0.233	-0.236
Shear force (N)	**-0.226**	**-0.526**	-0.568	0.510	0.429	0.383	0.250	-0.363	**-0.207**	-0.378	0.212	0.525	0.223	**0.040**	0.000	0.379

*Correlation values in bold within the same row indicate significant differences ($P < 0.05$).

Values in bold have a p-value of > 0.5.

4 Discussion

The sensory profile of warthog back bacon was dominated by typical bacon and smoky aromas and flavours, and salty flavour. The sensory profile and FA composition of the LL muscle were influenced by the process of bacon production, which are different to that determined for cooked warthog LL in Chapter 5. To summarize, the bacon had a sensory profile which compares to that of pork bacon regarding aroma and flavour, while tenderness, juiciness and shear force values did not differ between sex or age class, although the residue and appearance of fibres did. Similar to the findings in Chapter 5, there were no differences in the chemical composition between sex and age for the back bacon after cooking, with the moisture content higher, and the protein and fat content lower compared to back bacon produced from South African pig breeds (Hoffman, Styger, Muller, & Brand, 2005). The most notable differences in chemical composition between uncured and cured warthog LL is the increase in total moisture and ash content, and decrease in total protein content, which is expected as the processing method introduces moisture and salt (Table 1). The fatty acid composition of the bacon also appears to be influenced by processing and storage (± 3 weeks at -20ºC), with an increase in the proportion of MUFA and a decrease in the proportion of SFA and PUFA (Table 5). The higher MUFA content is attributed to the higher content of oleic acid (C18:1n9t), while it is noted that elaidic acid was not found in this analysis (Table 6), which were present in cooked warthog LL (Chapter 5) albeit at very low levels (0.03 $mg \cdot g^{-1}$). It is suggested that elaidic acid was not detected as it was present at levels lower than detection threshold of the technique used. While fat content and FA composition primarily determines the volatiles produced in fresh meat during cooking, the aromatic volatiles develop from lipid degradation and the Maillard reaction, and from interaction between the processes, producing a number of aromatic volatiles that may contribute to the flavour profile (Mottram, 1998). In addition, the addition of nitrite in cured meat products is considered to influence the aromatic volatiles through suppression of lipid oxidation and reactivity with FA during cooking (Timón, Carrapiso, Jurado, & van de Lagemaat, 2004).

Since the meat of warthogs have been associated with sensory attributes described as 'sour/sweaty' or 'fishy', this study provides evidence that processes such as curing and smoking can be used to reduce or 'mask' undesirable flavours in meat, thereby converting the meat into a desirable product. As mentioned, the meat from wild animals is associated with a gamey or livery taste, while game meat and the meat from non-ruminants is typically high in total unsaturated FA (UFA) content and thus more susceptible to lipid oxidation (Faustman et al., 2010), which leads to undesirable aromas and flavours. Van Schalkwyk, McMillin, Booyse, Witthuhn and Hoffman (2011) found gamey flavour was not associated with cured smoked salami made from different game meats, and suggested that smoking reduces perceived game flavour in processed products. A cured, smoked sausage known as cabanossi in South Africa was produced with warthog meat and did not affect consumer preference compared to the same sausage produced with commercial pork (Swanepoel, Leslie, Hoffman, 2016, Chapter 9). Here, it is suggested that the addition of nitrite greatly affect the lipid oxidation during cooking, which determines the volatile compounds produced responsible for flavour. The intramuscular fat (IMF) content is generally low in the meat of game species (Neethling, Hoffman, & Muller, 2016), which primarily consists of structural lipid components, phospholipids and cholesterol, with high proportions of PUFA (Fisher et al., 2000). The meat from free-ranging grazers have a higher PUFA, and n-3 in particular, content compared to farmed animals fed concentrate diets, as animals extensively feeding on grasses incorporate more n-3 and n-6 PUFA fatty acids in their muscles (Valencak & Gamsjäger, 2014). As PUFA oxidize more readily than SFA, meat high in total PUFA is more susceptible to lipid oxidation (Faustman et al., 2010) and the development of associated off-aromas and flavours which decreases meat quality and desirability. As mentioned, processes such as curing, smoking and addition of spices are used to inhibit the rate of oxidation and subsequent development of off-aromas and flavours, as well as imparting specific flavours (Gandemer, 2002). Nitrite as an anti-oxidant stabilizes the heme-iron group of the myoglobin molecule, chelates metal ions and radicals and reacts with UFA (Sebranek & Bacus, 2007), while certain phenolic compounds produced from wood-smoking scavenge oxygen radicals (Kjällstrand & Petersson, 2001).

Hydrocarbons, aldehydes, ketones and alcohols derived from thermal degradation and Maillard reactions are primarily associated with pork flavour, and to a lesser extent, pyrazines, furans, and pyridines (Timón et al., 2004), as the oxidation of unsaturated fatty acids produce significant quantities of carbonyl compounds (ketones and aldehydes) (Shahidi, 1998). Similar aromatic compounds are found in uncured and cured pork but at much lower concentrations in cured pork which help explain the difference in flavour profiles (Mottram, 1984, 1998, Ramarathnam, Rubin, & Diosady, 1991). The lower concentrations is attributed to the suppression of lipid oxidation by nitrite, while certain compounds including pyrazines, pyridines, furans and nitriles were only present or present at higher concentrations in cooked cured pork (Timón et al., 2004). These organic nitrite compounds are suggested to contribute to the characteristic flavour of bacon, or in combination with other compounds, which are produced through the interactions between and reactivity of nitrite and FA (Mottram, 1984, Timón et al. 2004). Pyrazines are the major products of the Maillard reaction and it has been suggested that phospholipids significantly participate in the Maillard reaction which produces heterocyclic compounds (Farmer & Mottram, 1990, Mottram, 1998). Since phospholipids consist primarily of PUFA, this could explain the desirable bacon flavour profile lean meats such as warthog obtain following processing.

Cured flavour, described here as typical bacon flavour, is the most important characteristic of nitrite-cured meat products, although the dynamics of the flavour development is not fully understood (Andersen, 2004). This flavour is considered a preservation of the fresh meat flavour combined from the retardation of rancidity development in salted meat products, as salting meat accelerates proteolysis and lipolysis which causes the development of rancid aromas and flavours. However, salting also imparts a desirable salty flavour. In addition to nitrites, smoking also reduces lipid oxidation and microbial spoilage (Andersen, 2004). The majority of volatile compounds are derived from smoking and responsible for smoky flavour (Poligne, Collignan, & Trystram, 2002), which cause the meat to have a very different aromatic profile compared to fresh pork or hams (Yu & Sun, 2005). While phenols primarily contribute to smoky flavour, aldehydes, ketones and alcohols have also been implicated in smoky flavour (Yu, Sun, Tian, & Qu, 2008). The low scores for the fishy and sour/sweaty aroma and flavour of warthog bacon is ascribed to the processing methods used, and these attributes do not contribute to the overall sensory profile of warthog back bacon.

In addition, it is known that meat high in PUFA is undesirable for bacon production (and storage) as the hardness of fat is reduced, which causes difficulties during slicing of bacon as uniform rashers. (Andersen, 2004). While the PUFA proportion of warthog meat and bacon is higher compared to domestic pigs, the actual content ($mg \cdot g^{-1}$) is very low (Table 6) (Enser, Hallett, Hewitt, Fursey, & Wood, 1996, Wood et al., 2008). Therefore the low PUFA content might have a negligible impact on slicing quality. In addition, wild suids may include higher levels of Vitamin E in their diet which improves oxidative stability of the meat (Quaresma et al., 2011), although Vitamin content has not yet been determined for warthog meat. In contrast, Crawford, Gale, and Woodford (1970) found the adipose tissue of warthogs to consist primarily of palmitic, stearic (SFA, 31%), oleic (MUFA, 20%) and linoleic and linolenic (PUFA, 34%). The warthogs from this investigation had a minimum of subcutaneous fat (data not given), although earlier observations (Swanepoel et al., 2014, Chapter 5) has shown that warthogs can develop a significant subcutaneous fat cover depending on season and food availability. Although the total content ($mg \cdot g^{-1}$) of the FA is not known, it is suggested that if present the subcutaneous fat layer is removed prior to processing as the fat may contribute to rancidity and slicing quality of warthog back bacon.

As noted by Sampels, Pickova, and Wiklund (2004), the chemical composition of smoked meat products depends on the smoking method used. For example, excessive dehydration may occur with hot smoking at temperatures of >60ºC (Fernandes et al., 2014), and lipolysis with drying at 40ºC. Sampels et al. (2004) found that curing and smoking as preservation process influenced the total fat content to a greater extent than the FA composition of reindeer meat. The fat content decreased following lipolysis at smoking chamber temperatures of 80ºC and internal meat core temperatures of 65ºC. The weight losses following smoking averaged around 8.5% but there was only a slight reduction in fat content in warthog back bacon, which is expected considering the overall low fat content of warthog meat (Chapter 6, 8) and the low smoking temperatures used. Game meat, characterized by a lean profile, therefore lends itself well as an alternative meat for producing reduced fat processed products. The warthog cabanossi had a reduced fat product compared to the pork but with similar sensory attributes (Swanepoel, Leslie, Hoffman, 2016, Chapter 9). Not all products are suited for fat reduction strategies, as fat-reduced products should still satisfy consumers' expectations regarding distinctive visual qualities, display a level of familiarity, and with the added benefit of being healthier and organic (Grunert & Valli, 2001, Radder & le Roux, 2005), whilst not compromising eating quality, safety and production costs (Colmenero, 2000, Grasso, Brunton, Lyng, Lalor, & Monahan, 2014)

Gullett, Partlow, Fisher, Halina, and Squires (1993) suggested that texture and liking of bacon was influenced by the method of preparation, and therefore did not attempt to evaluate the liking of texture as 'doneness' of bacon is a personal preference. Neethling et al. (2016) noted that the differences in sample preparation and description of sensory attributes complicates the comparison between the results of studies. Here, the cooking method and presentation to panellists was different compared to other studies on bacon in order to standardize sensory analysis. The moist cooking of bacon as a whole muscle and presentation to the panellists as a cube of meat is suggested to allow for the perception of juiciness, tenderness and appearance of bacon. Despite the different scores for appearance of muscle fibre bundles between sex and age, the scores for juiciness and tenderness was high for warthog bacon and did not differ between sexes or age class. It is noted that the total pick up % and smoking loss % was lower and higher, respectively, for the warthog bacon compared to commercially produced bacon where the desired average pick up is 20% and smoking loss <5%. The differences in the total pick up %, total weight change %, total ash content and appearance is ascribed to the size (weight) and myofibre composition of the muscles between sexes and age class, while processing is ultimately considered responsible for the sensory profile of warthog back bacon. It is suggested that the high moisture content and low cooking loss of warthog back bacon contributed to the initial and sustained juiciness, as cooking loss was negatively associated with moisture content. The addition of salt increases the water holding capacity (WHC) during cooking, and also the separation of the protein bundles in muscle fibres which weakens the muscle fibres and loosening of myofibrillar lattice, which contributes to tenderness appearance of cured products (Ruusunen & Puolanne, 2005).

During mastication, the total moisture contributes to initial juiciness, while fats stimulate saliva secretion and total fat content therefore contributes to sustained juiciness (Lawrie & Ledward, 2006). However, the desired flavour compounds produced during the Malliard reactions further stimulates saliva secretion which could contribute to perceived juiciness (McGee, 1984). The desired compounds in bacon are associated with attributes described as 'bacon', 'fried meat', 'roast meat' and 'cooked meat-like' (Timón et al., 2004). According to Tshabalala, Strydom, Webb, and De Kock (2003), the aromatic compounds in lean meat become more volatile and are readily released with water vapour, which are encountered during orthonasal analyses.

A PUFA:SFA ratio of ≥ 0.45 and omega 6:omega 3 (ω6:ω3) of ≤ 4 is recommended for the meats consumed by humans (Warris, 2000) as a diet high in unsaturated FA provides health benefits. Warthog back bacon has an improved PUFA:SFA and omega 6:omega 3 ratio compared to South African pig and ostrich bacon, and other smoked meat products (Table 8). Although there were differences between sex and age class, all of the ratios fell within the desired range. Warthog back bacon is also an example of how processed meat products can be developed that meets global health recommendations in terms of low total fat and SFA content. However, the final salt and nitrite content of the bacon was not determined in this study, and future research should determine this as it could have implications for product production, marketing and labelling. Apart from the recommendation for decreased fat and SFA consumption, there has been concern raised regarding the consumption of red meat and processed product consumption, with calls made for lower salt and nitrite content in processed products.

Table 8: The fatty acids composition (%) of warthog muscle, warthog back bacon other products.

Sample	SFA (%)	MUFA (%)	PUFA (%)	PUFA:SFA	ω6:ω3	Total fat (%)
Warthog loin[a]	41.3	2.4	56.3	1.4	2.9	1.2
Warthog back bacon[b]	36.5	12.4	49.4	1.37	3.32	1.3
Pork back bacon[c]	43.3	47.3	9.4	0.2	8.6	8.4
Smoked reindeer[d]	36.3	34.0	29.4	0.9	5.9	3.3

[a]Chapter 5.
[b]This study.
[c]Hoffman et al. (2005b).
[d]Sampels et al. (2004).

5 Conclusion

The results from this study indicate that warthog meat can be utilized in processed products with health benefits without compromising the sensory attributes associated with bacon. The study provides evidence that processes such as curing and smoking can be used to reduce or 'mask' undesirable flavours in meat, thereby converting the meat into a desirable product. The addition of nitrite and contribution of smoking compounds are suggested responsible for this conversion, and the development of desirable aromatic compounds associated with bacon. It is suggested that the production of processed game meat products should consider physical parameters including age and gender as these affect the size and structure of muscles which could influence the production yields, although this did not appear to ultimately influence the sensory profile of warthog back bacon. Increased utilization of warthog meat has been proposed as a strategy to encourage warthog control and population management, and the utilization of the meat in processed products could broaden the scope of wildlife utilization and game meat consumption.

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7 References

AOAC International (2002a) Official methods of analysis. Arlington, Virginia, USA: Association of Official Analytical Chemists Inc. Loss on drying (moisture) at 95–100°C for feeds. (17th ed.) AOAC Official Method 934.01.

AOAC International (2002b) Official methods of analysis. Arlington, Virginia, USA: Association of Official Analytical Chemists Inc. (17th ed.). Ash of Animal Feed. AOAC Official Method 942.05

AOAC Official Method 992.15 (1992). Crude protein in meat and meat products including pet foods. Combustion method. *Journal of Association of Official Analytical Chemists International*, 76, 787.

Andersen, H. J. (2004). Bacon production. In W. K. Jensen, D. Carrick, & M. Dikeman (Eds.), *Encyclopedia of meat sciences* (pp. 51–59). Oxford, UK: Elsevier Ltd.

Banon, S., Costa, E., Gil, M., & Garrido, M. (2003). A comparative study of boar taint in cooked and dry-cured meat. *Meat Science*, *63*, 381–388. Retrieved from http://www.sciencedirect.com/science/article/pii/S0309174002000979

Bender, A. (1992). Meat and meat products in human nutrition in developing countries. FAO and INPhO, Food and Nutrition Paper 53. Rome, Italy: Food and Agriculture Organization of the United Nations. Retrieved from http://www.fao.org/docrep/t0562e/t0562e00.HTM.

Bouvard, V., Loomis, D., Guyton, K. Z., Grosse, Y., El Ghissassi, F., Benbrahim-Tallaa, .L,…& Straif, K. (2015). Carcinogenicity of consumption of red and processed meat. *The Lancet Oncology, 16*, 1599–1600. doi.org/10.1016/S1470-2045(15)00444-1.

Burger, J. (2002). Daily consumption of wild fish and game: exposures of high end recreationists. *International Journal of Environmental Health Research*, *12*, 343–354. doi:10.1080/0960312021000056393

Colmenero, F. J. (2000). Relevant factors in strategies for fat reduction in meat products. *Trends in Food Science & Technology*, *11*, 56–66. Retrieved from http://www.sciencedirect.com/science/article/pii/S092422440000042X

Crawford, M. A., Gale, M. M., & Woodford, M. H. (1970). Muscle and adipose tissue lipids of warthog, *Phacochoerus aethiopicus*. *International Journal of Biochemistry*, *1*, 654–658. doi:10.1016/0020-711x(70)90039-x

Department of Agriculture, Forestry and Fisheries (DAFF). (2013). *South African Yearbook 2012/13: Agriculture, Forestry and Fisheries*. In A. Vermeulen (Ed.) (pp 44–82). Pretoria, South Africa: Department of Agriculture, Forestry and Fisheries. Retrieved from http://www.gcis.gov.za.

Enser, M., Hallett, K., Hewitt, B., Fursey, G. A. J., & Wood, J. D. (1996). Fatty acid content and composition of english beef, lamb and pork at retail. *Meat Science*, *42*, 443–456. doi:10.1016/0309-1740(95)00037-2

Farmer, L. J., & Mottram, D. S. (1990). Interaction of lipid in the Maillard reaction between cysteine and ribose: The effect of a triglyceride and three phospholipids on the volatile products. *Journal of the Science of Food and Agriculture*, *53*, 505–525. doi:10.1002/jsfa.2740530409

Faustman, C., Sun, Q., Mancini, R., & Suman, S. P. (2010). Myoglobin and lipid oxidation interactions : Mechanistic bases and control. *Meat Science*, *86*, 86–94. doi:10.1016/j.meatsci.2010.04.025

Fernandes, V. R. T., Souza Franco, M. L. R., Mikcha, J. M. G., de Souza, V. L. F., Gasparino, E., Coutinho, M. E., … Del Vesco, A. P. (2014). Yacare caiman (*Caiman yacare*) trim hamburger and sausage subjected to different smoking techniques. *Journal of the Science of Food and Agriculture*, *94*, 468–72. doi:10.1002/jsfa.6270

Fisher, A. V, Enser, M., Richardson, R. I., Wood, J. D., Nute, G. R., Kurt, E., … Wilkinson, R. G. (2000). Fatty acid composition and eating quality of lamb types derived from four diverse breed x production systems. *Meat Science*, *55*, 141–147. doi:10.1016/S0309-1740(99)00136-9

Folch, J., Lees, M., & Sloane-Stanley, G. H. (1957). A simple method for the isolation and purification of total lipids from animal tissues. *Journal of Biological Chemistry*, *226*, 495-509.

Gandemer, G. (2002). Lipids in muscles and adipose tissues, changes during processing and sensory properties of meat products. *Meat Science*, *62*, 309–321. doi:10.1016/S0309-1740(02)00128-6

Geldenhuys, G., Hoffman, L. C., & Muller, M. M. (2014). Sensory profiling of Egyptian goose (*Alopochen aegyptiacus*) meat. *Food Research International*, *64*, 25–33. doi:10.1016/j.foodres.2014.06.005

Girolami, A., Napolitano, F., Faraone, D., Di Bello, G., & Braghieri, A. (2014). Image analysis with the computer vision system and the consumer test in evaluating the appearance of Lucanian dry sausage. *Meat Science*, *96*, 610–616. doi:10.1016/j.meatsci.2013.08.006

Grasso, S., Brunton, N. P., Lyng, J. G., Lalor, F., & Monahan, F. J. (2014). Healthy processed meat products – Regulatory, reformulation and consumer challenges. *Trends in Food Science & Technology*, *39*, 4–17. doi:10.1016/j.tifs.2014.06.006

Grunert, K. G., & Valli, C. (2001). Designer-made meat and dairy products: Consumer-led product development. *Livestock Production Science*, *72*, 83–98. doi:10.1016/S0301-6226(01)00269-X

Gullett, E. A., Partlow, D., Fisher, K. R. S., Halina, W. G., & Squires, E. J. (1993). Effect of pig sex on consumer ratings for pork chops and bacon. *Food Quality and Preference*, *4*, 201–205.

Hoffman, L. C., & Cawthorn, D.-M. (2012). What is the role and contribution of meat from wildlife in providing high quality protein for consumption? *Animal Frontiers*, *2*, 40–53. doi:10.2527/af.2012-0061

Hoffman, L. C., Crafford, K., Muller, N., & Schutte, D. W. (2003). Perceptions and consumption of game by a group of tourists visiting South Africa. *South African Journal of Wildlife Research*, *33*, 125–130.

Hoffman, L. C., Muller, M., Schutte, D. W., Calitz, F. J., & Crafford, K. (2005a). Consumer expectations , perceptions and purchasing of South African game meat. *South African Journal of Wildlife Research*, *35*, 33–42.

Hoffman, L. C., & Sales, J. (2007). Physical and chemical quality characteristics of warthog meat. *Livestock Research for Rural Development*, *19,* Article 153. Retrieved from http://www.lrrd.org/lrrd19/10/hoff19153.htm

Hoffman, L. C., Styger, E., Muller, M., & Brand, T. S. (2005b). Sensory , physical and chemical quality characteristics of bacon derived from South African indigenous and commercial pig breeds. *South African Journal of Animal Science*, *6*, 36–48.

Honikel, K. O. (1998). Reference methods for the assessment of physical characteristics of meat. *Meat Science*, *49*, 447–457. doi:10.1016/S0309-1740(98)00034-5

Kiley-Worthington, M. (2014). Ecological agriculture. Integrating low input , high productive farming with wildlife conservation: Results from the experimental farm La Combe , Drome France. *Open Journal of Ecology*, *4*, 744–763.

Kjällstrand, J., & Petersson, G. (2001). Phenolic antioxidants in wood smoke. *Science of The Total Environment*, *277*, 69–75. doi:10.1016/S0048-9697(00)00863-9

Koster, J. M., Hodgen, J. J., Venegas, M. D., & Copeland, T. J. (2010). Is meat flavor a factor in hunters' prey choice decisions? *Human Nature*, *21*, 219–242. doi:10.1007/s12110-010-9093-1

Lawless, H. T., & Heymann, H. (2010). *Sensory evaluation of food: Principals and practises* (2nd ed.). New York: Chapman & Hall.

Lawrie, R. A., & Ledward, D. A. (2006). *Lawrie's meat science* (7th ed.). Cambridge, England: Woodhead Publishing.

Lee, C.M., Trevino, B. & Chaiyawat, M. (1996). A simple and rapid solvent extraction method for determining total lipids in fish tissue. *Journal of AOAC International, 79*, 487–492.

Macmillan, D. C., & Phillip, S. (2008). Consumptive and non-consumptive values of wild mammals in Britain. *Mammal Review*, *38*, 189–204. doi:10.1111/j.1365-2907.2008.00124.x

Marino, R., Albenzio, M., Della Malva, A., Muscio, A., & Sevi, A. (2015). Nutritional properties and consumer evaluation of donkey bresaola and salami: Comparison with conventional products. *Meat Science*, *101*, 19–24. doi:10.1016/j.meatsci.2014.11.001

Mason, D. R. (1984). Dentition and age determination of the Warthog *Phacochoerus aethiopicus* in Zululand, South Africa. *Koedoe*, *27*, 79–119.

McGee, H. (1984). *On food and cooking* (1st ed.). New York, USA: Scribner.

Mottram, D. S. (1984). Organic nitrates and nitriles in the volatiles of cooked cured pork. *Journal of Agricultural and Food Chemistry*, *32*, 343–345.

Mottram, D. S. (1998). Flavour formation in meat and meat products : A review. *Food Chemistry*, *62*, 415–424.

Neethling, J., Hoffman, L. C., & Muller, M. M. (2016). Factors influencing the flavour of game meat: A review. *Meat Science*, *113,* 139–153.

Nyafu, K. (2009). *Warthog as an introduced species in the Eastern Cape*. MSc thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

Paleari, M. A., Moretti, V. M., Beretta, G., Mentasti, T., & Bersani, C. (2003). Cured products from different animal species. *Meat Science*, *63*, 485–9. doi:10.1016/S0309-1740(02)00108-0

Poligne, I., Collignan, A., & Trystram, G. (2002). Effects of salting, drying, cooking, and smoking operations on volatile compound formation and color patterns in pork. *Journal of Food Science*, *67*, 2976–2986. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2621.2002.tb08848.x/abstract

Quaresma, M. A. G., Alves, S. P., Trigo-Rodrigues, I., Pereira-Silva, R., Santos, N., Lemos, J. P. C., … Bessa, R. J. B. (2011). Nutritional evaluation of the lipid fraction of feral wild boar (*Sus scrofa scrofa*) meat. *Meat Science*, *89*, 457–461. doi:10.1016/j.meatsci.2011.05.005

Radder, L., & Le Roux, R. (2005). Factors affecting food choice in relation to venison: A South African example. *Meat Science*, *71*, 583–9. doi:10.1016/j.meatsci.2005.05.003

Ramarathnam, N., Rubin, L. J., & Diosady, L. L. (1991). Studies on meat flavor. 2: A quantitative investigation of the volatile carbonyls and hydrocarbons in uncured and cured beef and chicken. *Journal of Agricultural and Food Chemistry*, *39*, 1839–1847. doi:10.1021/jf00010a031

Rødbotten, M., Kubberød, E., Lea, P., & Ueland, Ø. (2004). A sensory map of the meat universe. Sensory profile of meat from 15 species. *Meat Science*, *68*, 137–44. doi:10.1016/j.meatsci.2004.02.016

Ruusunen, M., & Puolanne, E. (2004). Histochemical properties of fibre types in muscles of wild and domestic pigs and the effect of growth rate on muscle fibre properties. *Meat Science*, *67*, 533–539. doi:10.1016/j.meatsci.2003.12.008

Sampels, S., Pickova, J., & Wiklund, E. (2004). Fatty acids, antioxidants and oxidation stability of processed reindeer meat. *Meat Science*, *67*, 523–32. doi:10.1016/j.meatsci.2003.12.006

Sebranek, J. G., & Bacus, J. N. (2007). Cured meat products without direct addition of nitrate or nitrite: what are the issues? *Meat Science*, *77*, 136–147. doi:10.1016/j.meatsci.2007.03.025

Shahidi, F. (1998). Flavour of muscle foods - An overview. In F. Shahidi (Ed.), *Flavour of Meat, Meat Products and Seafoods*. (2nd ed.). London, UK: Blackie Academic and Professional.

Shapiro, S., & Wilk, M. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, *52*, 591–611. Retrieved from http://www.jstor.org/stable/2333709

Swanepoel, M., Leslie, A. J., & Hoffman, L. C. (2014). The influence of season and sex on the carcass yield of common warthog (*Phacochoerus africanus*). *South African Journal of Wildlife Research*, *44*, 179–188.

Swanepoel, M., Leslie, A. J., & Hoffman, L. C. (2016). Comparative analyses of the chemical and sensory parameters and consumer preference of a semi-dried smoked meat product (cabanossi) produced with warthog (*Phacochoerus africanus*) and domestic pork meat. *Meat Science, 114*, 103–113. doi:10.1016/j.meatsci.2015.12.002.

Timón, M. L., Carrapiso, A. I., Jurado, A., & van de Lagemaat, J. (2004). A study of the aroma of fried bacon and fried pork loin. *Journal of the Science of Food and Agriculture*, *84*, 825–831. doi:10.1002/jsfa.1740

Tshabalala, P. A., Strydom, P. E., Webb, E. C., & De Kock, H. L. (2003). Meat quality of designated South African indigenous goat and sheep breeds. *Meat Science*, *65*, 563–570. doi:10.1016/S0309-1740(02)00249-8

Tuorila, H. M., Meiselman, H. L., Cardello, A. V, & Lesher, L. L. (1998). Effect of expectations and the definition of product category on the acceptance of unfamiliar foods. *Food Quality and Preference*, *9*, 421–430. doi:10.1016/S0950-3293(98)00012-3

Valencak, T., & Gamsjäger, L. (2014). Lipids in tissues of wild game: overall excellent fatty acid composition, even better in free- ranging individuals. In P. Paulsen, A. Bauer, & F. J. M. Smulders (Eds.), *Trends in Game Meat Hygiene* (pp. 335–344). Wageningen, Germany: Wageningen Academic Publishers. doi:10.3920/978-90-8686-238-2

Van Schalkwyk, D. L., McMillin, K. W., Witthuhn, R. C., & Hoffman, L. C. (2010). The contribution of wildlife to sustainable natural resource utilization in Namibia: A review. *Sustainability*, *2*, 3479–3499. doi:10.3390/su2113479

Van Schalkwyk, D. L., McMillin, K. W., Booyse, M., Witthuhn, R. C., & Hoffman, L. C. (2011). Physico-chemical, microbiological, textural and sensory attributes of matured game salami produced from springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*), kudu (*Tragelaphus strepsiceros*) and zebra (*Equus burchelli*) harvested in Namibia. *Meat Science*, *88*, 36–44. doi:10.1016/j.meatsci.2010.11.028

Van Schalkwyk, D. L., & Hoffman, L. C. (2010). *Guidelines for the Harvesting of Game for Meat Export*. Windhoek, Namibia: Printech.

Voisey, P. W. (1976). Engineering assessment and critique of instruments used for meat tenderness evaluation. *Journal of Texture Studies, 7*, 11-48

Warris, P. (2000). *Meat Science*. Oxon: CAB Publishing.

Wood, J. D., Enser, M., Fisher, A. V, Nute, G. R., Sheard, P. R., Richardson, R. I., … Whittington, F. M. (2008). Fat deposition, fatty acid composition and meat quality: A review. *Meat Science*, *78*, 343–358. doi:10.1016/j.meatsci.2007.07.019

Yu, A.-N., & Sun, B.-G. (2005). Flavour substances of Chinese traditional smoke-cured bacon. *Food Chemistry*, *89*, 227–233. doi:10.1016/j.foodchem.2004.02.029

Yu, A.-N., Sun, B.-G., Tian, D.-T., & Qu, W.-Y. (2008). Analysis of volatile compounds in traditional smoke-cured bacon (CSCB) with different fiber coatings using SPME. *Food Chemistry*, *110*, 233–238. doi:10.1016/j.foodchem.2008.01.040

Chapter 9

Comparative analyses of the chemical and sensory parameters and consumer preference of a semi-dried smoked meat product (cabanossi) produced with warthog (*Phacochoerus africanus*) and domestic pork meat*

Abstract

The study compared the chemical and sensory characteristics and consumer preference of a semi-dried, cured meat product, cabanossi, produced with warthog meat and with domestic pork. The warthog and pork cabanossi had similar total moisture (59.0% ± 2.07 and 54.3% ± 1.26) and protein (26.3% ± 2.20 and 24.2% ± 2.15) contents, while the warthog cabanossi was lower in total fat content (6.9% ± 1.01) compared to pork cabanossi (13.7% ± 1.77, $P = 0.007$). Descriptive sensory analysis found the warthog cabanossi appeared darker red ($P = 0.001$) and less fatty ($P = 0.001$), while the pork cabanossi had a higher overall pork flavour ($P = 0.001$). There were no differences in consumer preference of the appearance and taste between the two types of cabanossi, while the majority consumers (91%) supported the use of game meat in meat products. The study concluded that warthog meat can be used in processed products without compromising the associated technical or organoleptic properties.

Keywords: warthog, game meat, meat products, sensory, consumer, cabanossi

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1 Introduction

Producing meat from wild animals has been suggested as a low-input, high production alternative to traditional animal husbandry (Hoffman & Cawthorn, 2012). Promoters of game meat consumption maintain that utilizing wild animals contributes towards sustainable wildlife and habitat management and local food security, while generating an income from a widely available resource (Van Schalkwyk, McMillin, Witthuhn, & Hoffman, 2010). It is important to note that the utilization of game meat for human consumption is based on the premise that the meat is harvested from wild animals in a sustainable manner, and wild populations are managed to promote growth and stability. This type of harvesting is not similar to bushmeat hunting in parts of Africa where certain animal species are intensely and illegally hunted by humans for food, which have caused local species extinctions or severe reductions of distribution ranges (Hoffman & Cawthorn, 2012). Game meat destined for the formal market is produced by farms and reserves that farm with or hunt wild animals, and is also a by-product of hunting for recreation, population management or problem animal control purposes. In Namibia, safari hunting accounts for the majority of game meat produced (Van Schalkwyk et al., 2010, Lindsey et al., 2013). More than 95% of the game meat produced annually (between 15 917 000 and 24 952 000 kg) is consumed within the country allowing for 87% of livestock meat produced to be exported. During the six month hunting season, game meat contributes approximately 10% of red meat utilized per annum in South Africa, which was estimated at around 1 249 000 kg during 2011/2012 (Dry, 2010, Department of Agriculture, Forestry and Fisheries [DAFF], 2013).

A growing body of scientific literature have highlighted the superior carcass and meat quality parameters of game animals (Van Zyl & Ferreira, 2004, Mostert & Hoffman, 2008, Hoffman, Kroucamp, & Manley, 2007a, Hoffman, Smit, & Muller, 2008, Hoffman, 2008, Dannenberger, Nuernberg, Nuernberg, & Hagemann, 2013, Bartoň, Bureš, Kotrba, & Sales, 2014). Game animals in general produce a lean and healthy meat, which is high in protein, low in fat with a favourable fatty acid profile. The low overall lipid content and fatty acid composition is largely attributed to their forage diet and high levels of activity (Valencak & Gamsjager, 2014). Despite the relative slow growth of the game meat industry, consumers and producers have increasingly become aware of the health attributes of game meat in general and its value as a sustainable red meat source (MacMillan & Phillip, 2008). Game meat is also consider exotic, which is attractive to consumers who are adventurous and pursue new culinary experiences, and to foreign tourists who want to consume meat from native animals (Hoffman, Crafford, Muller, & Schutte, 2004, Hoffman, Muller, Schutte, Calitz, & Crafford, 2005) or take products home as souvenirs. Exotic meat enjoys the interest of the social elite where it is marketed in affluent restaurants as a highly valued, and priced, commodity (Adams, 2000).

The common warthog (*Phacochoerus africanus*) has historically been hunted and consumed by rural communities throughout its large distribution range across Africa. The species has become an extra-limital invasive in parts of South Africa through introduction and range expansion. Since warthogs are a known agricultural pest, they are hunted by agricultural producers for damage reprisal (Nyafu, 2009). This practise produces a carcass of which the meat can be used for human consumption. Similar to other game species, warthogs have a high dressing percentage, low total intramuscular lipid content, high total protein and moisture content and a favourable fatty acid profile (Hoffman & Sales, 2007, Swanepoel, Leslie, & Hoffman, 2014). The general carcass yield of common warthogs and other wild ungulates average around 56-66% for mature (adult) animals of both sexes (Hoffman 2007), and around 65.5% for wild boars (*Sus scrofa*), Skewes, Morales, Mendoza, Smulders, & Paulsen, 2008). However, the dressed carcass weights of wild boars normally include the head and skin, while the warthogs and domestic pigs include the head, trotters and skin (with most of the adjoining subcutaneous fat). If the head, skin and trotters are included in the dress out percentages for warthogs, they are similar to those for domestic pigs ready for slaughter in South Africa (74.2-79.2 %, and 77.8% respectively) (Pieterse, 2009, Swanepoel et al. 2014). While the body weight of ungulate species are inherently different, intraspecies variation in dress out percentages is influenced by gut fill, diet and muscle (carcass) leanness. Furthermore, the diet of monogastric Suidae greatly influences the lipid content and fatty acid profile of the meat (Wood et al. 2008).

Game meat has the reputation of being difficult to prepare, thus processed products that are convenient or ready-to-eat might have more appeal for consumers and further expand the market for game meat through value-adding (Hoffman et al., 2004). Preservation processes such as curing, drying or fermentation aims to increase the shelf-life of meat products which makes them more readily available to consumers (Van Schalkwyk, McMillin, Booyse, Witthuhn, & Hoffman, 2011). The development of game meat products should consider sensory, technological, safety and nutritional aspects of the product (Colmenero, 2000). This study aimed to develop a game meat product using warthog meat, to determine the chemical and sensory characteristics and consumer acceptability.

2 Materials and Methods

2.1 Slaughtering and sampling

The warthog meat was obtained from farms in the Boshoff farming district (28°33’0”S, 25°14’0”E) near Bloemfontein in the Free State province (Ethical clearance number: 11LV_HOF02) in 2011. The blesbok (*Damaliscus pygargus phillipsi*) meat was sourced from Brakkekuil farm (34°18’24”S, 20°49’3”E) near Witsand in the Western Cape (Ethical clearance number: 10NP_HOF02) in 2010. Fifteen free-roaming warthogs and 32 blesbok were shot using a single shot bolt action rifle. The warthog group consisted of eight adult females, two adult males, one juvenile female and four juvenile males, and the blesbok group of 12 adult females and 20 adult males. Shots were placed in the head, neck or flank (aiming for the heart). The animals were exsanguinated and allowed to bleed out in the field before being transported to a slaughtering facility and dressed according to the *Guidelines for the Harvesting of Game for Meat Export* (Van Schalkwyk & Hoffman, 2010). The carcasses were chilled for 24 hours at 4°C before the meat from all the animals (except the *Longissimus thoracis et lumborum, Biceps femoris, Semimembranosus, Semitendinosus, Infraspinatus* and *Supraspinatus* muscles) were removed, vacuum packed and frozen at -4°C for processing. The meat was transported with a cooling truck at 4°C to Stellenbosch University where it was stored in a freezer at -20°C. The pork buttocks, consisting of *Biceps femoris*, *Semimembranosus* and *Semitendinosus* muscles, and back fat from six pigs were sourced from a commercial abattoir (Winelands Pork, Bellville, South Africa). The meat and fat were randomly obtained from Large white sows and barrows pigs weighing between 90-100 kg.

2.2 Cabanossi processing

The product, cabanossi (alternative spelling kabanosy), is a type of cured and cold smoked sausage stick consumed as a ready-to-eat snack in South Africa. It is thin (± 1 cm in diameter) and medium in length (± 30 cm) (Schoon, 2012). It is similar to another popular South African dried sausage, droëwors (Hoffman, Jones, Muller, Joubert, & Sadie, 2013), except that cabanossi is smoked and semi-dried. For comparative purposes, another cabanossi was produced using commercially reared pork. The sensory properties and preference of the two types of cabanossi were compared using both a trained sensory panel and a consumer preference tests. The sensory analysis evaluated the cabanossi in terms of visual appearance, aroma, taste and texture, and the consumer analysis evaluated consumer preference of visual appearance and taste. The product needs to satisfy consumers' expectations regarding distinctive visual and sensory qualities, attain a level of similarity to the product they are familiar with, with the added benefit of being healthier and organic (Radder & Le Roux, 2005). However, reducing the fat content should not have detrimental effects on eating quality, safety and production costs (Colmenero, 2000). Three batches of pork and warthog cabanossi were made (N=6). The recipe and spices for the cabanossi was sourced from a commercial producer, Deli Spices™ (25 Bertie Avenue, Epping 2, Cape Town, South Africa). The recipe produced a 15 kg batch and three batches of each type was produced (Table 1). The meat was trimmed of excess fat and sinew, and the meat and fat was cut into 10x10 cm blocks before being minced separately through a 12 mm diameter sieve, after which the meat, fat and spices for each 15kg batch was mixed by hand.

The mixture was then minced through a 5 mm diameter sieve as an additional mixing step. The mixture was stuffed into natural sheep casings (18-22 mm in diameter). The raw cabanossi were then smoked and dried in a commercial smoker Reich Airmaster® UKF 2000 BE (Reich Klima-Räuchertechnik, Urbach, Germany) with a SmartSmoker and TradiSmoker LS 500 HP electronic, automatically controlled by a Microprocessor (Unicontrol 2000). The program cycles and order are given in Table 2. Eight randomly selected cabanossi links of each batch were weighed before and after smoking to determine smoking loss. All the smoked links from each batch were vacuum packed and stored at 4ºC. During production, randomly selected samples (10g) of each raw ingredient (meats) and product (unsmoked and smoked cabanossi) of the separate batches were taken, vacuum packed and stored at -20ºC for chemical analyses. The smoked warthog (sWC) and pork (sPC) cabanossi was the final product used for the sensory and consumer panel evaluations. The unsmoked warthog and pork cabanossi are abbreviated as uWC and uPC, respectively.

Table 1: Recipe used for cabanossi production.

Ingredients	Kg	%
Batch size	15	100
Warthog meat/Pork	7	46.6
Blesbok meat	6.5	43.3
Pork fat	1	6.6
Spice mixture	0.6	4
Ice water	0.5	3.3

Table 2: The smoking cycle parameters for cabanossi production.

Activity	Temperature (ºC)	Relative humidity (%)	Time (hours)
Reddening	40	80	2.00
Drying	30	30	2.00
Cold smoking	30	20	0.30
Smoke destruction	30	30	0.10
Drying	30	30	2.00
Cold smoking	30	20	0.20
Smoke destruction	30	20	0.10
Drying	30	30	8.00

2.3 Proximate analyses

For the proximate analyses, a 10g sample of warthog meat, pork, blesbok meat, and pork fat, as well as samples of the unsmoked and smoked warthog and pork cabanossi were individually homogenized for 3 min to create a representative sample, vacuum packed and stored at -20ºC. The samples were thawed overnight (12h) at 4°C before chemical analysis. The mean total moisture, ash and crude protein content (%) was determined according to the Association of Official Analytical Chemist's Standard Techniques (AOAC) method 934.01 (moisture content), method 942.05 (ash content) and the Dumas combustion method 992.15 (crude protein content) (AOAC 2002a, 2002b, 2002c, respectively). Total moisture content was determined using a 2.5 g homogenized sample. The moisture-free sample was used to determine total ash content. A 0.15 g, defatted, dried and finely ground sample was used for crude protein analysis with a Leco Nitrogen/Protein Analyser (FP – 528, Leco Corporation). Before the analyses the machine was calibrated using 0.15 g ethylenediamineteraacetic acid (EDTA) samples (Leco Corporation, 3000 Lakeview Avenue, St. Joseph, MI 49085-2396, USA, Part no.502-092, Lot no. 1055). After 20-30 analyses the machine was calibrated again with EDTA samples. The percentage Nitrogen (% N) per sample was given and multiplied by a conversion factor of 6.25 to calculate the total crude protein content per sample. The chloroform/methanol extraction method as described by Lee et al. (1996) was used to determine the total lipid content using a 5 g sample. The warthog and blesbok meat used for the cabanossi production were analysed using a chloroform/methanol 1:2 v/v solution, while the pork meat, pork fat and the uncooked and cooked cabanossi samples were analysed using a chloroform/methanol 2:1 v/v solution. All analyses were performed in duplicate. The laboratory at the Department of Animal Sciences, Stellenbosch University, is accredited by the Agricultural Laboratory Association of South Africa (AgriLASA) to perform accurate and reliable proximate analyses and for validation of accuracy and repeatability partakes in monthly inter-laboratory blind tests.

2.4 Fatty acid analysis

The fatty acids (FA) were extracted and analysed according to the method described by Folch, Lees, and Sloane-Stanley (1957). Chloroform/methanol (1:2 v/v) solution was used for extraction of a 2 g homogenized sample. The extraction solution contained 0.01 % butylated hydroxytolene (BHT) to act as an anti-oxidant. The 2 g meat sample and 20 ml solution was homogenized using a polytron mixer (Kinematica, type PT 10–35, Switzerland). Heptadecanoic acid (C17:0) was added (0.5 ml) to the extracted fat sample as an internal standard in order to quantify the observed fatty acids in the sample (Internal standard: Catalogue number H3500, Sigma-Aldrich Inc., 3050 Spruce Street, St. Louis, MO 63103, USA). A 250 µL sub-sample of the extraction was transmethylated for 2 h at 70°C in a water-bath using a methanol/sulphuric acid (19:1, v/v) as transmethylating agent (2 ml). The transmethylated sample was cooled to room temperature before the fatty acid methyl esters (FAME) were extracted by adding 1 ml dH_2O and 2 ml hexane to the sample and transferring the top hexane layer. The sample was dried under nitrogen at 45 °C, after which 50 µL hexane was added. A 1 µL of the FAME sample was injected into a Thermo Finnigan Focus gas-chromatograph (GC) (Thermo-Electron S.p.A, Rodana, Milan, Italy), equipped with a flame ionized detector and a 60 m BPX70 capillary column (internal diameter 0.25 mm, 0.25 µm film, SGE International, Ringwood, Victoria, Australia). The flow rate of the hydrogen gas carrier was 30 mL/min with the following temperature settings: initial temperature 60ºC, injector 220ºC, detector 260ºC and final temperature 160ºC. The injection volume of the GC was 1 µL with an approximate run time of 45 minutes. The FAME values were determined by comparing the FAME samples with a standard FAME mixture (Supelco, 37 Component FAME mix C4-C24, Cat, no. 47885-U. Supelco, North Harrison Rd, Bellefonte, PA 16823-0048, USA). Results were calculated as the total percentage fatty acids present in one gram of tissue and as $mg.g^{-1}$ since the amount of internal standard (C17:0) was known.

2.5 Descriptive sensory analysis

A panel of 10 judges were trained according to Lawless and Heymann (2010) using generic descriptive techniques. The panellists were recruited from a pre-existing group of judges involved with research studies on meat and other food stuffs at Stellenbosch University. During two one hour long training sessions the panellists made use of reference samples to formulate a list of sensory attributes. The reference samples included two types of commercial pork cabanossi, cooked warthog S*emitendinosus* muscle, liquid smoke solution, smoked snoek (*Thyrsites atun)* and pickled herring (*Clupeidae* spp.), all sourced from commercial retailers. Fourteen sensory attributes were identified (Table 3). The cabanossi was evaluated by the trained panellists during two blind-tasting sessions (three hour sessions, divided into 90 min sessions) that scored each attribute on an unstructured 100-point scale. The project was presented to, and the data collected from, panellists using Compusense® five software (Compusense, Guelph, Canada) whilst seated in booths in a temperature and lighting controlled room. For sample preparation the cabanossi were cut into 4cm pieces and placed in glass ramekins for presentation and sampling. The samples were evaluated at room temperature. For statistical purposes, the 10 panellists each received 2 samples of each of the 3 batches of warthog and pork cabanossi for comparison per session (n = 2), resulting in 12 replications (n=12) per judge and 120 evaluations in total.

Table 3: Definition and scale of each attribute used for the descriptive sensory analysis of cabanossi.

Characteristic	Sensory attribute	Description	Reference
Aroma*	Smoky aroma	Aroma associated with smoked meat products	Liquid smoke solution
Appearance	Appearance of fat	Appearance of visible fat particles 0 = Few; 100 = Many	Commercial cabanossi
	Colour	Red associated with cured sausages 0 = Light red; 100 = Dark red	Commercial cabanossi
	Texture	Appearance of minced meat in casing 0 = Very fine; 100 = Very grainy	Commercial cabanossi
Flavour*	Pork flavour	Flavour associated with cured pork products	Commercial cabanossi
	Game flavour	Associated with game meat	Warthog meat
	Fishy flavour	Associated with fish	Pickled herring and smoked snoek
	Smoky flavour	Associated with smoked meat products	Liquid smoke solution
	Saltiness	Level of saltiness	Salt solution
	Peppery flavour	Black peppercorn flavour	Commercial cabanossi
	Toughness	Impression of toughness after 5 chews 0 = Tender; 100 = Tough	Commercial cabanossi
	Juiciness	Impression of juiciness (due to fattiness) after 5 of chews (0 = Dry; 100 = Juicy)	Commercial cabanossi
	Firmness	Impression of firmness of the meat texture after 5 chews (0 = Gooey; 100 = Firm)	Commercial cabanossi
	Residue	Amount left after 5 chews, due to presence of sinew, before swallowing sample (0 = None; 100 = Abundant sinew)	Commercial cabanossi

*Scale for descriptors: 0 = Low, 100 = High, unless otherwise stated. Aroma and flavour were analysed orthonasally and retronasally, respectively.

2.6 Cabanossi consumer analysis

The pork and warthog cabanossi were subjected to a consumer evaluation (n = 96) of untrained participants during the poster session of the South African Wildlife Management Association's (SAWMA) annual symposium. One 4 cm sample of each treatment was given to participants in clear plastic petri dishes marked with colour stickers to distinguish between the two types. The consumers were asked to complete a questionnaire determining their liking of the taste and the appearance of the product. The questionnaire is made available as Supporting Information. Their opinions regarding game meat consumption and preference, as well as attitudes towards hunting and utilization of game meat in meat products (in particular warthog meat) were asked. Samples from all 6 batches (sWC = 3 and sPC = 3) were randomly given to consumers. The taste and appearance evaluations were measured on a 9 point scale, where 1 = Dislike extremely, 5 = Neutral and 9 = Like extremely.

2.7 Statistical analysis

The data obtained from the sensory and chemical experiments were statistically analysed with STATISTICA (StatSoft, Inc. 2013, version 12). The chemical data were analysed using one-way analysis of variance (ANOVA) with species as fixed factor and batch as random effect(s). The sensory experiment was treated as a random block design, with two treatments, three samples (batches) and two replications per sample, resulting in 12 total replications per treatment. All sensory data were analysed using mixed model repeated measures ANOVA with judge and batch as random factors, and treatment as fixed effects. The equation of the model for the experimental design is given as:

$$y_{ij} = \mu + \beta_j + t_i + \varepsilon_{ij}$$

where μ = overall mean, β_j = the effect of the block, t_i = the effect of the treatment, ε_{ij} = the error associated with the block and treatment. The consumer data was analysed using mixed model repeated measures ANOVA with the same fixed and random effects. For post hoc testing, Fisher's LSD was used when the main effects/interactions analysed were significant. Outliers were identified from normal probability plots, and removed where deemed necessary. A 5% level of significance was used as a guideline for explaining significantl differences. Pearson's correlation and principal component analyses (PCA) were also performed on for the chemical and sensory attribute values.

3 Results

Since each ingredient and batch consisted of meat from animals of different genders and seasons, it is therefore expected to observe variation among the chemical composition of each batch, and high standard deviation in the means of the meat ingredients and subsequent products. The fatty acid values of one batch sPC (Batch 2) was removed from final analysis as the fatty acid values differed significantly from the other two sPC batches (Batch 1 and 3), which could not be explained by variation in the raw ingredients and is therefore most likely a sampling error.

3.1 Chemical analysis

The mean moisture loss from smoking was 36.0% (± SE, 1.02) for sWC and 35.4% (± 1.12) for sPC. The mean moisture, protein, fat and ash content of the raw ingredients and cabanossi products are presented in Table 4. Pork was lower in moisture content than warthog ($P = 0.002$) and blesbok ($P = 0.001$) meat, and higher in lipid content compared to warthog ($P = 0.026$) and blesbok ($P = 0.017$) meat. There was no difference between uWC and uPC regarding chemical composition, while the moisture content decreased in sWC ($P = 0.006$) and sPC ($P = 0.011$) and the fat content increased as a result of the drying process. Although not significant, the uWC was lower in total fat content than the uPC but the different losses in moisture content resulted in the fat content of the sPC becoming significantly higher. Also, while the protein contents of both cabanossi increased following drying, only the protein content of sWC increased significantly ($P = 0.06$) from that of uWC. Furthermore, the high fat and ash content (P =0.049) of sPC is attributed to the high fat and ash content of pork which became concentrated following moisture loss.

3.2 Fatty acid profile

The fatty acid (FA) composition of the raw ingredients and the products are presented in Table 5. The most abundant fatty acids in both warthog meat and pork (in descending order) were oleic, palmitic, linoleic and stearic acid, with both species meats being similar in saturated (SFA) content (39.8 and 39.4%, respectively) but not polyunsaturated PUFA content (34.7 and 22.9%, respectively). Blesbok meat had high stearic and palmitic acid content which contributed to a high total SFA content (57.4%), whilst pork fat consisted primarily of oleic acid (74.4%), resulting in high monounsaturated MUFA content (75.0%).

Warthog meat had the highest linoleic acid content which differed from blesbok meat ($P = 0.01$) but not from pork ($P = 0.57$), while warthog meat, pork and blesbok meat had similar proportions of λ- linolenic acid which was significantly lower in pork fat ($P < 0.001$). Warthog and blesbok meat had the highest α-linolenic (ALA) content compared to pork and pork fat ($P < 0.01$). Pork, warthog and blesbok were similar regarding eicosatrienoic (C20:3n6) acid content, while warthog meat had the highest proportion of eicosatrienoic acid (C20:3n3) ($P > 0.001$). Warthog and blesbok meat had the highest proportion of eicosapentaenoic acid (EPA) ($P < 0.01$) but there was no difference in the proportion of docosapentaenoic acid (DPA) or docosahexaenoic acid (DHA) acid between pork, warthog and blesbok meat.

Warthog meat had a higher proportion of MUFA and PUFA compared to pork ($P = 0.001$ and $P = 0.025$, respectively) and the highest polyunsaturated:saturated fatty acid ratio (PUFA:SFA), which differed from blesbok meat ($P = 0.011$); the high total SFA content of blesbok meat resulted in the low PUFA:SFA ratio. Pork and pork fat did not differ from warthog or blesbok meat regarding the PUFA:SFA ratio ($P > 0.05$). The high content of α-linolenic acid in warthog and blesbok meat resulted in a low omega 6:omega 3 (n-6:n-3) ratio compared to the high ratio for pork and pork fat. There was no difference in the fatty acid profile of the two types of cabanossi before or after smoking. In terms of total FA content ($mg.g^{-1}$), the sWC had significantly lower palmitic, stearic, oleic, y- linolenic, λ-linolenic and docosapentaenoic acid content compared to the sPC (Table 5). The total SFA, MUFA and PUFA content of the sPC, but not the sWC, increased significantly following smoking.

Table 4: The mean (% ± SE) chemical composition of the ingredients and cabanossi before and after smoking.

	Meat ingredients				Products			
	Warthog	Pork	Blesbok	Pork fat	uWC	uPC	sWC	sPC
Moisture	$71.9^{a} \pm 4.08$	$59.1^{b} \pm 4.26$	$74.4^{a} \pm 1.52$	$55.3^{b} \pm 1.15$	$69.8^{a} \pm 0.37$	$68.1^{a} \pm 0.80$	$59.0^{b} \pm 2.07$	$54.3^{b} \pm 1.26$
Protein	$24.0^{ab} \pm 2.88$	$29.5^{a} \pm 1.40$	$21.1^{b} \pm 0.83$	-	$20.4^{a} \pm 0.56$	$19.7^{a} \pm 1.74$	$26.3^{b} \pm 2.20$	$24.2^{ab} \pm 2.15$
Fat	$3.3^{a} \pm 1.20$	$8.8^{b} \pm 2.22$	$2.9^{a} \pm 0.57$	$49.4^{c} \pm 1.75$	$4.9^{a} \pm 0.83$	$7.7^{a} \pm 2.22$	$6.9^{a} \pm 1.01$	$13.7^{b} \pm 1.77$
Ash	$1.2^{ab} \pm 0.01$	$2.1^{a} \pm 1.10$	$1.1^{ab} \pm 0.01$	$0.4^{b} \pm 0.04$	$3.3^{ab} \pm 0.08$	$3.2^{a} \pm 0.07$	$4.6^{ab} \pm 0.63$	$4.6^{b} \pm 0.21$

$^{a, b, c}$Means in rows for meat components and products, respectively, with different superscripts differ significantly ($P < 0.05$).

Table 5: Fatty acid composition (mg·g⁻¹ ± SE) of the raw ingredients and the cabanossi before and after smoking.

Fatty acid	Raw ingredient: Warthog	Pork	Blesbok	Pork fat	Product: Unsmoked warthog cabanossi	Unsmoked pork cabanossi	Smoked warthog cabanossi	Smoked pork cabanossi*
C16:0	7.3^{c} ± 2.40	19.4^{b} ± 4.81	5.8^{c} ± 1.37	47.2^{a} ± 2.10	12.0^{b} ± 2.48	18.3^{b} ± 5.48	17.2^{b} ± 3.06	36.1^{a} ± 3.17
C18:0	5.3^{c} ± 1.90	13.7^{b} ± 3.93	10.2^{bc} ± 2.68	22.1^{a} ± 0.41	11.7^{b} ± 5.25	11.2^{b} ± 2.65	13.9^{b} ± 2.57	23.9^{a} ± 3.55
C18:1n9c	8.1^{c} ± 3.60	31.5^{b} ± 8.34	4.4^{c} ± 0.18	367.2^{a} ± 9.83	12.7^{b} ± 0.46	26.8^{b} ± 8.14	18.6^{b} ± 2.82	50.2^{a} ± 7.22
C18:2n6c	6.8^{bc} ± 2.67	15.7^{b} ± 3.78	3.2^{c} ± 0.30	44.0^{a} ± 5.19	5.9^{b} ± 0.59	12.5^{ab} ± 3.81	9.8^{ab} ± 1.67	22.6^{a} ± 2.30
C18:3n6	0.1^{c} ± 0.03	0.2^{b} ± 0.06	0.1^{c} ± 0.01	0.4^{a} ± 0.05	0.1^{b} ± 0.01	0.1^{b} ± 0.04	0.1^{b} ± 0.02	0.3^{a} ± 0.03
C18:3n3	1.32^{b} ± 0.55	0.61^{b} ± 0.13	1.10^{b} ± 0.23	2.34^{a} ± 0.35	0.62 ± 0.09	0.86 ± 0.23	1.01 ± 0.07	1.79 ± 0.04
C22:5n3	0.5 ± 0.23	0.3 ± 0.08	0.4 ± 0.10	0.2 ± 0.03	2.4^{b} ± 0.64	2.4^{b} ± 0.81	3.4^{b} ± 0.14	6.6^{a} ± 0.42
C22:6n3	0.1^{b} ± 0.05	0.2^{b} ± 0.03	0.1^{b} ± 0.02	0.3^{a} ± 0.04	0.04^{b} ± 0.02	0.1^{b} ± 0.02	0.1^{ab} ± 0.04	0.2^{a} ± 0.01
Total SFA	13.02^{c} ± 4.33	34.8^{b} ± 9.14	16.6^{bc} ± 4.13	74.1^{a} ± 2.77	24.9^{b} ± 8.21	31.03^{b} ± 8.72	32.6^{b} ± 5.87	62.8^{a} ± 7.04
Total MUFA	8.7^{c} ± 3.91	33.0^{b} ± 8.33	4.8^{c} ± 1.33	369.9^{a} ± 9.91	13.8^{b} ± 0.44	28.8^{b} ± 8.73	20.02^{b} ± 3.0	54.1^{a} ± 7.61
Total PUFA	11.6^{bc} ± 4.24	19.9^{b} ± 4.80	7.1^{bc} ± 0.94	49.6^{a} ± 5.92	10.0^{b} ± 0.77	17.4^{b} ± 4.80	16.1^{b} ± 1.72	35.0^{a} ± 2.76

^{a,b,c}Means in rows with different superscripts differ significantly ($P < 0.05$) for raw ingredients and product, respectively.

*N = 2

3.3 Sensory attributes

The sensory profile of the smoked warthog and pork cabanossi is presented in Table 6. It is noted that there were differences among the batches per cabanossi type. The first batch of sWC appeared darker red than the second and third batch in terms of colour ($P < 0.05$), while the first batch of sPC appeared grainier than the second batch of sPC in terms of appearance ($P = 0.015$). Overall, the sPC appeared fattier ($P = 0.001$) and lighter red ($P = 0.001$) with a more distinct pork flavour ($P = 0.006$) than sWC, while sWC had a more distinct game meat flavour ($P = 0.002$). However, due to the low scores given for game flavour (8.8 ± 1.17) it makes a negligible contribution to the flavour profile of sWC. There were no other major sensorial differences detected between the two types of cabanossi, while it was expected that the scores for smoky aroma and flavour would be similar since the cabanossi was subjected to the same smoking programme. There were also no differences for salty and peppery flavours, due to the fact that the same spice mixture was used according to the prescribed recipe. The panellist did not detect "fishy-flavour" in any of the samples.

Table 6: The sensory attributes* (mean % ± SE) of cabanossi made from warthog meat and pork.

Sensory attribute	sWC	sPC
Smoky aroma	56.2± 0.49	55.3 ± 0.82
Appearance of fat	40.3^{a} ± 1.16	46.8^{b} ± 1.41
Colour	73.4^{a} ± 1.31	68.0^{b} ± 0.84
Texture	44.6 ± 0.32	46.0 ± 0.88
Pork flavour	50.9^{a} ± 1.29	57.6^{b} ± 0.78
Gamey flavour	8.8^{a} ± 1.17	5.0^{b} ± 0.47
Smoky flavour	58.1 ± 0.56	59.01 ± 0.11
Saltiness	43.7 ± 0.91	44.9 ± 0.50
Peppery flavour	64.2 ± 0.68	64.7 ± 0.76
Toughness	34.7 ± 0.40	34.0 ± 0.28
Juiciness	44.7 ± 0.22	46.2 ± 0.48
Firmness	44.9 ± 1.01	44.3 ± 0.27
Residue	17.1 ± 0.54	16.6 ± 0.66

[a, b] Means in rows with different superscripts differ significantly ($P < 0.05$).

3.4 Principle component analysis

Principle component analysis (PCA) was conducted for the chemical and sensory attributes according to the different batches of cabanossi sampled (Figure 1), with the outlier batch sPC2 not included. Principle component 1 (PC 1) accounted for 44.2% of the total variation and PC 2 for 26.9%. PC 1 showed separation between taste attributes pork flavour and game flavour, and appearance attributes colour (darker red) and percentage fat (fattier appearance), and a positive association of game flavour with colour, and pork flavour with percentage fat. PC 1 also showed clear separation of sWC and sPC, while principle component 2 (PC 2) shows the separation of sWC 1 and sWC 2 from sWC 3.

Pearson correlation between the chemical and sensory variables of the cabanossi revealed a number of general associations. The percentage visible fat as assessed by panellists was positively associated with visible texture (grainier, R-value of 0.96), pork flavour (0.97), and total fat content (0.88), whilst associating negatively with colour (lighter red, -0.99). Pork flavour was associated with total percentage fat (0.84) and to a lesser degree with total MUFA content (0.70). As expected, salty and peppery flavour was associated with total ash content (0.81 and 0.83, respectively), whilst textural toughness was linked to peppery flavour (0.83) and total protein content (0.93). Initial juiciness was positively associated with total fat content (0.88) and negatively with total protein content (-0.86). Finally, textural firmness was linked to the amount of residue left in the mouth after chewing (0.93).

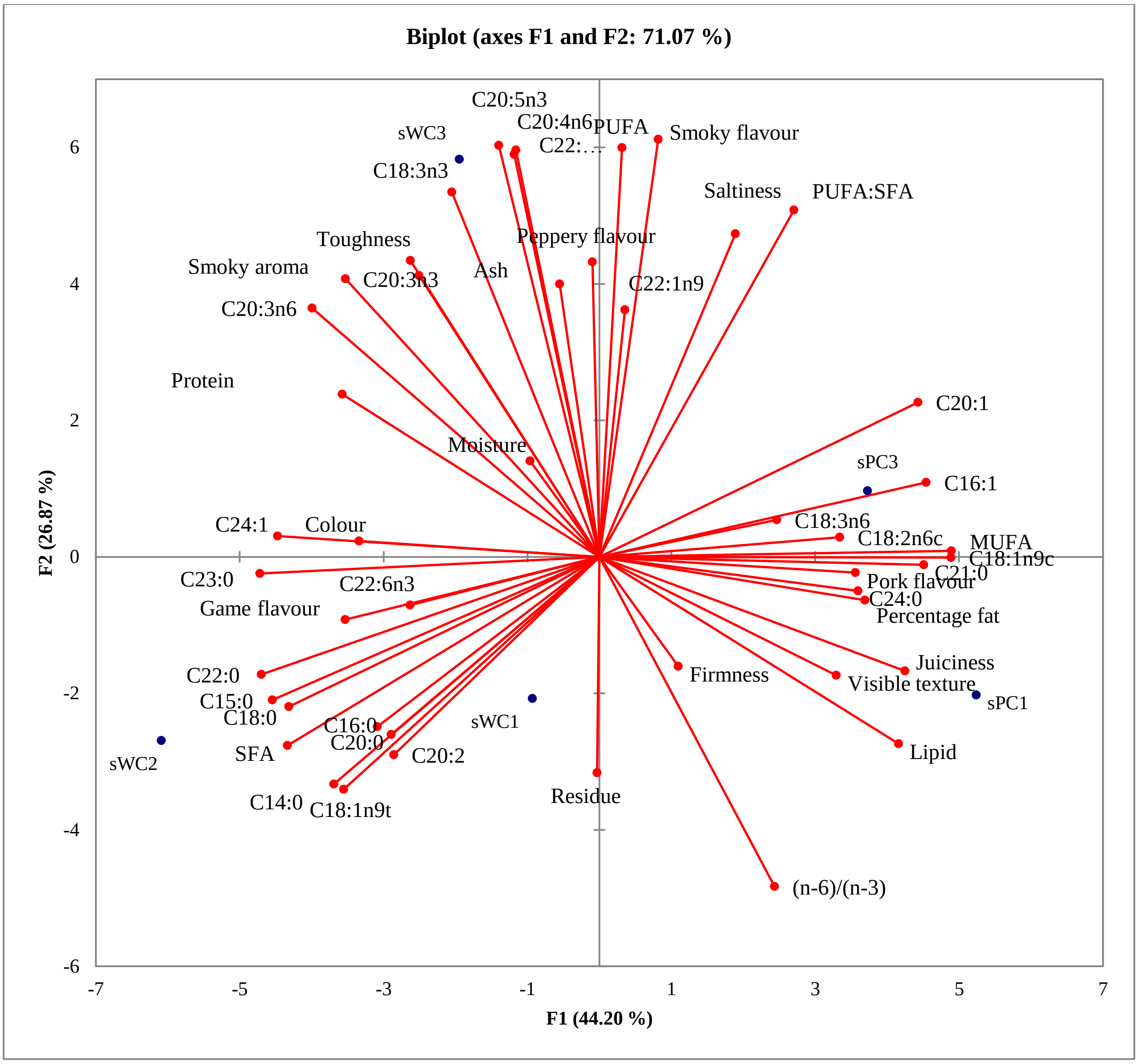

Figure 20: Principle component analysis of the chemical and sensory attributes of smoked warthog (sWC, N = 3) and pork (sPC, N = 2) cabanossi.

3.5 Consumer analysis

The demographic results from the consumer panel and the attributes they associate with game meat (higher values denote higher association) are depicted in Table 7. The majority of the respondents were male, Caucasian and between the ages of 18 and 20. Most held a degree obtained from a tertiary institution and were involved with nature conservation in some manner. Healthy and tasty were attributes positively associated with game meat, while gamey and organic received less consideration. The mean scores for the warthog and pork cabanossi regarding appearance was 6.8 (± 0.15) and 6.9 (± 0.13) respectively, and regarding taste was 6.9 (± 0.15) and 7.1 (± 0.13), respectively. There was no statistical difference between the warthog and pork cabanossi regarding appearance and taste, or among batches. None of the demographic variables (gender, age, education and involvement in conservation) in this study influenced the scores given for the warthog and pork cabanossi, while ethnicity was excluded in the analysis due to the high imbalance of the sampled population

Game meat is consumed weekly by 50% of the respondents, monthly by 15%, once or twice a year by 30% while 4% of the respondents have never consumed any form of game meat. The majority of respondents (42%) have never eaten any form of warthog meat. The most frequently consumed game meat product was biltong, which is a popular South African air-dried meat product, typically made using beef or game meat. The majority (89%) supported hunting as wildlife management tool and the use of game meat in commercially available meat products (91%). Thirty-six percent of the respondents were hunters, and springbok (*Antidorcas marsupialis)* was the game species most often hunted (19 responses), followed by greater kudu (*Tragelaphus strepsiceros*) (8 responses) and impala (*Aepyceros melampus*) (7 responses). Springbok and kudu was the game meat species most frequently consumed.

Table 7: The demographics of the consumer panel and the mean ratings (± SE) of the attributes consumers' associated with game meat.

Aspect	%
Gender	
Male	68
Female	32
Age class	
18-20	38
21-25	18
26-30	21
35-40	11
45-50	12
Ethnicity	
Caucasian	81
Black	11
Coloured	6
Indian	1
Education	
High school	20
Higher tertiary degree	80
Involvement in conservation	
Yes	72
No	28
Associated attributes	Mean ratings (± SE)
Tasty	$7.2^{a} \pm 0.20$
Healthy	$7.1^{a} \pm 0.23$
Lean	$6.5^{b} \pm 0.27$
Gamey	$5.9^{b,c} \pm 0.25$
Organic	$5.8^{c} \pm 0.29$

[a,b,c]Values with different superscripts within the same column are significantly ($P < 0.05$) different for the associated attributes.

4 Discussion

Overall, warthog and blesbok meat were high in protein and low in total lipid content, similar to the meat of other wild ungulates including impala (*A. melampus*), kudu (*T. strepsiceros*) (Hoffman, Mostert, Kidd, & Laubscher, 2009), red hartebeest (*Alcelaphus buselaphus caama*) (Hoffman, Smit, & Muller, 2010), springbok (*A.marsupialis*) (Hoffman, Kroucamp, & Manley, 2007b) and wild boar (*Sus scrofa*) (Dannenberger et al., 2013). This adheres to the general composition of lean meat, which constitutes of > 70% moisture, > 20% protein and < 3 % fat content. The chemical composition of the pork used here was slightly different to those of South African pork loins as determined by Pieterse (2006), with lower total moisture (< 60%) and higher total fat content (> 5%).

The most abundant fatty acids found in all the raw ingredients were palmitic, oleic and stearic acids, which are the major fatty acids found in animal meat (Enser, Hallett, Hewitt, Fursey, & Wood, 1996). The oleic and subsequent MUFA content of the pork fat used in this study was high compared to the those found by other authors (Enser et al. 1996), but it is known that the fatty acid content of commercially reared pork and adipose tissue is influenced by diet, rearing conditions, age and total carcass fat (Olssen & Pickova, 2005). As the accumulation of fatty acids in the adipose tissue increases over time, the MUFA content increases as the SFA content decreases from the continuing desaturation of SFA to their MUFA counterparts (Wood et al., 2008), with oleic acid the product of desaturated stearic acid. Feeding pigs a diet high in oleic acid also increases the content of this FA in adipose tissue (Klingenberg, Knabe & Smith, 1995).

Warthog meat and pork had similar high levels of linoleic acid content, a PUFA found in high levels in domestic pork and pork fat (Wood et al., 2004). Hoffman and Sales (2007) also found high levels of linoleic acid (26.12%) in warthog loins. This FA passes through single stomach animals unchanged after ingestion to be incorporated into tissues, while in ruminant animals, the majority is biohydrogenated to SFA and therefore occurs in lower proportions in muscle tissue (Jenkins, 1993). Linoleic together with ALA and λ- linolenic acid are essential FA as they are obtained solely from the diet. In this study, warthog and blesbok meat had higher levels of α-linolenic acid (ALA) than pork which is likely a result of their primarily grass-based diet, since ALA is the major fatty acid of grasses (Dungait, Docherty, Straker, & Evershed, 2010). The intake and composition of this fatty acid may therefor differ in wild herbivore muscle due to the seasonal and regional variability of grasses, which means that products produced with game meat are likely to inherently vary in chemical composition. Most of the ALA is also biohydrogenated to SFA in ruminant animals. The high SFA content of the blesbok meat is largely attributed to the high total palmitic and stearic, and low total linoleic acid content of the meat. While linoleic acid is derived solely from the diet as mentioned, palmitic and stearic acid is synthesized *de novo* in ruminant animals by specific ruminal microbes (Jenkins, 1993). The extent to which these SFA are synthesized depends on the conditions of the rumen, such as N-content and feed particle size, but it is known that high quantities of linoleic acid inhibit complete hydrogenation to stearic acid. The lower PUFA:SFA ratio of the blesbok meat in this study was attributed to the elevated SFA content. Neethling, Britz and Hoffman (2014) found higher mean PUFA:SFA ratios for blesbok meat (0.96), but determined that muscle type, animal gender and season influences the FA composition of the meat. All of the raw ingredients had PUFA:SFA ratios above that of the recommended ≥ 0.45 for meat products, while the omega 6:omega 3 (n-6:n-3) ratio of blesbok and warthog meat fell within the range found for other game meat species (Hoffman et al., 2010, Neethling et al., 2014), which is also in agreement with the recommended ≤ 4 for meat products (Warris, 2000).

The high protein and low lipid content of warthog and blesbok meat produced a cabanossi that was high in total protein content similar to the pork cabanossi, but significantly lower in total lipid content. Both the sWC and sPC however had a lower total fat content compared to the maximum of 40% fat content allowed for cold smoked cured sausages according to the South African National Standard (SANS 885:2011). As noted by Samples, Pickova and Wiklund (2004), the chemical composition of smoked meat products depends on the smoking method used. In this study, the smoking and drying cycles were characterized by low chamber temperatures (maximum of 40ºC) which is different to the production parameters used for traditional cabanossi production, where hot smoking at 60-70ºC is applied to reach internal core temperatures of ± 65ºC (Tyburcy & Kozyra, 2010). However, excessive dehydration may occur with hot smoking at temperatures of 60ºC (Fernandes et al., 2013), and lipolysis with drying at 40ºC (Samples et al., 2004), and cold smoking was applied to prevent "over-drying" of the product, considering the low total fat content of the game meats used (warthog and blesbok). The final product still had a desirable moisture content of < 60% for cabanossi (Tyburcy & Kozyra, 2010).

Despite the lower total fat content of sWC, there were no significant differences in the FA profile of the two types of cabanossi before and after smoking. This is attributed to the addition of 6.6% pork fat, while the relatively unchanged UFA content before and after smoking indicates that significant lipid oxidation did not occur during the smoking process. Lipid peroxidation is a relatively common occurrence in processed meat products (Hoffman et al., 2013), but curing and smoking are both processes used to inhibit the rate of oxidation and subsequent development of off-aromas and flavours. Nitrite as an anti-oxidant stabilizes the heme-iron group of the myoglobin molecule, chelates metal ions and radicals and reacts with UFA (Sebranek & Bacus, 2007), while certain phenolic compounds produced from wood-smoking scavenge oxygen radicals (Kjällstrand & Petersson, 2001). While ascorbic acid was the functional ingredient of the spice mix used to promote colour development and prevent colour fading (by accelerating the reduction of metmyoglobin to nitrosommyoglobin), the colour of nitrate cured products may not always be uniform even when standard production methods are used (Girolami, Napolitano, Faraone, Di Bello, & Braghieri, 2014). For example, the suspension of curing chemicals phosphate and ascorbic acid in the brine mixture affects nitrite content and curing results in the final product. Here however, the inherent variation in raw materials was deemed responsible for the visual differences among the cabanossi batches. It is suggested that either the warthog or blesbok meat used for the first sWC batch consisted of muscles with higher myoglobin content which resulted in a darker red product. It would be useful for future studies to measure pH and instrumental colour values of both raw and final products if it is to be evaluated for colour during sensory analysis, in order to pre-establish possible variances.

The visual appearance of meat and meat products is one of the most important factors relating to consumers' expectations and willingness to purchase. Through visual perceptions consumers assess quality, freshness and eating sensation (Font-i-Furnols & Guerrero, 2014). Visible fat is a discerning factor at the point of purchase for consumers and most consumers show a preference for products with low amounts of visible fat, and are willing to pay more for these products if they are actually lower in fat as they associate this with increased quality (Girolami et al. 2014). The sPC appear fattier than sWC, indicating that the higher fat content of sPC was visually detectable to the panel. The sPC appeared lighter red than sWC which can also be attributed to the higher fat content of sPC, as fat content affects the colour of processed meat products, with high fat products appearing lighter, and low fat products darker and redder (Pietrasik, 1999). Pork meat is generally lighter in colour due to low levels of myoglobin pigment content which influences lightness (CIE L^*) and redness (CIE a^*) (Lindahl, Lundström, & Tornberg, 2001), while warthog meat is considered a 'red meat' due to high levels of myoglobin in wild animal muscles. This is also true of blesbok meat, which is a dark red meat with high CIE L^* (darker) and CIE a^* (redder) values (Hoffman et al., 2010). Although the colour profile and myoglobin content of warthog meat is yet to be determined, studies have found that wild boar meat is darker than pork with higher CIE a^* (redder) and lower CIE L^* (darker) values (Marchiori & Felício, 2003).

The composition of lipid tissues is largely considered responsible for the species-specific flavours of meat, while smoking, curing and the addition of spices influences flavour development by inhibiting or masking lipid oxidation and imparting specific flavours (Gandemer, 2002). The meat from wild animals is associated with a gamey or livery taste (Rødbotton, Kubberød, Lea, & Ueland, 2004), but it has been suggested that smoking reduces perceived game flavour in processed game meat products (Van Schalkwyk et al., 2011). The low scores given for game flavour for the sWC appear to agree with this suggestion, but there has been no sensory analysis conducted on unprocessed warthog meat to determine its overall flavour profile, and the associated gamey flavour specifically. Pork flavour has been positively associated with SFA and MUFA and negatively with PUFA (Wood et al. 2004). Here, the total SFA and MUFA content (mg.g^{-1}) was significantly higher in pork and pork fat compared to the game meats, and in the sPC compared to sWC, while the total PUFA content was not different for the pork, warthog and blesbok meat. Interestingly, the sensory panel detected no differences in juiciness and texture between the two types of cabanossi, despite the sPC having a significantly higher fat content. Both characteristics are associated with increased fat content in meat products, and it is possible that the low overall fat content of the two types of cabanossi have had negligible effect on these sensory characteristics. More marked differences might be observed in the fatty acid profiles and sensory characteristics if the proportion of warthog meat is increased and/or the amount of pork fat decreased.

The overall similarity between the two types of cabanossi was also reflected in the consumer analysis, where no distinction was found among consumer preferences for the appearance and liking of the two types of cabanossi. This indicates that products such as sWC can be produced and marketed as a low-fat alternative meat product. Although the majority of consumers have never eaten warthog meat, they do consume game meat on a relatively frequent basis, and generally associate the meat with positive health and taste attributes. Hoffman et al. (2005) found South African consumers positively associated game meat with leanness, healthiness and game flavour, and negatively with price, lack of availability, and game flavour. Black consumers in particular were more concerned about the “strong flavour” of game meat, while white consumers ate more game meat and associated the meat with health benefits. Burger (2002) found that gender, ethnicity and household income influences the amount of wild game and fish consumed among North American consumers. Overall, men consume more game and wild-caught fish than women, while black consumers consume more wild-caught fish than game, and wealthy households consume more deer than other game meat species. There were no such associations found in this study among demographic variables and consumption of game meat. This is perhaps due to most of the sampled consumer population being associated with wildlife conservation, and therefore more exposed to game meat utilization, or that the population was under representative of certain demographic groups. There has been no robust study focussing on the consumption of game meat among the diverse demographic groups in South Africa, and more research should be conducted to provide representative results on how South African consumers regard and utilize game meat.

Studies have found that consumers who hunt are more likely to regularly consume game meat than non-hunters, as are families with a hunter in the family (Radder & Le Roux, 2005), while hunters tend to prefer animal species whose meat they associate with an appealing flavour (Koster, Hodgen, Venegas, & Copeland, 2010). Hunters may therefor only hunt and consume the meat of a smaller number of species than those available to them, or only hunt those they are familiar with. The consumption of game meat is an important factor that promotes the social acceptability of hunting (Ljung, Riley, Heberlein, & Ericsson, 2012). Promoting public support for hunting is important since certain situations require the use of lethal methods for animal control (Koval & Mertig, 2004), and for the existence of a lucrative safari hunting industry. The wildlife species hunted and consumed by consumers in this consumer study were among the five most popular species hunted in South Africa (Warren, 2011). The aforementioned author suggested that game farms could increase their profitability by exposing hunters to a wider variety of game available for hunting on their farm. However, species introductions and translocations contribute to the homogenization of South African ungulate species compositions, with escapees (unintentional introductions) often forming established naturalized populations (Spear & Chown, 2008). The lack of a national framework which governs the practice of species introduction and translocation has recently been recognized by the Department of Environmental Affairs, who is in the process of developing a national framework for the norms and standards of translocation of indigenous Species (Notice 44 of 2015 National Environmental Management: Biodiversity Act, 2004).

Warthog meat has been compared to pork in terms of flavour and is considered to be of good eating quality (Somers, 1992). Utilizing the meat would not only contribute towards food security in the country but could also initialise a formal chain of warthog meat production for the commercial market whilst promoting sustainable wildlife utilization. There have however been reports that the fresh meat sometimes exhibits a flavour that is compared to "boar taint", an undesirable odour and taste which may occur in the meat from entire male domestic pigs (*S. scrofa*). This "boar taint" phenomenon has been associated with warthog meat from both genders and animals of different age classes, and warrants further investigation to determine the potential influence it might have on consumers' willingness to buy and consume warthog meat products. As mentioned, processing methods such as curing and smoking may potentially mask or reduce the formation of offensive volatile compounds (Bañón, Costa, Gil, & Garrido, 2003), and the results from this study are encouraging since there were no offensive flavours reported for the warthog cabanossi. Considering the popularity of game meat products such as biltong, developing processed game meat products is a potential strategy to introduce the meat of different game species to the commercial market. Further research should aim to investigate the physical, chemical and sensory parameters of warthog meat to determine its further potential use as a fresh or processed product.

The Food and Agriculture Organization of the United Nations and the World Health Organization (FAO/WHO, 2014) released a multi-criteria based ranking list of the most important food-borne parasites that pose a risk to humans. The parasites of warthogs that appear on the list in descending order of importance are *E. granulosus, Trichinella* spp., and *Sarcocystis* spp. All of these diseases are transmitted to humans when raw or undercooked meat from infected animals is ingested. Although warthogs are able to carry and transmit diseases to humans, there is a lack of documented cases of this occurring in southern Africa. It is possible that the majority of warthogs are harvested from outside of known zoonotic distribution ranges, and that potential zoonoses are effectively controlled through current disease management programs and control zones. In South Africa for example, *E. granulosus* appears to be limited to the northern bushveld region of the Limpopo province and Kruger National Park (KNP) (Van Wyk & Boomker, 2011), and *Sarcosystis* spp. associated with warthogs to the KNP

(Stolte et al., 1998). While studies on the prevalence of *Trichinella* infections among animals and humans is generally lacking in southern Africa, there has been no reports of *Trichinella* infections in domestic animals or humans in South Africa, Zimbabwe, Namibia or Mozambique (Pozio, 2007), and none among wild animals in South Africa outside of KNP. It should therefore be a continued effort to monitor for *Trichinella* infections in animals to prevent the introduction of the parasite elsewhere in South Africa.

5 Conclusion

The study found that warthog meat can be processed to produce a high-protein low-fat semi-dried product which consumers find acceptable without compromising the technical or organoleptic properties associated with the product. It serves as an example of how to introduce warthog meat to the commercial market in South Africa where game meat is enjoying increased attention as a healthy, low-input alternative to red meat. Value adding through processing also expands the potential of game meat for the commercial market.

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7 References

Adams, C. R. (2000). Social acceptability's role in an expanded rational expectations model of intention to consume an innovative meat product in a restaurant setting. *Journal of Hospitality and Tourism Research*, *24*, 252–262.

AOAC International (2002a) Official methods of analysis. Arlington, Virginia, USA: Association of Official Analytical Chemists Inc. Loss on drying (moisture) at 95–100°C for feeds. (17th ed.) AOAC Official Method 934.01.

AOAC International (2002b) Official methods of analysis. Arlington, Virginia, USA: Association of Official Analytical Chemists Inc. (17^{th} ed.). Ash of Animal Feed. AOAC Official Method 942.05

AOAC Official Method 992.15 (1992). Crude protein in meat and meat products including pet foods. Combustion method. *Journal of Association of Official Analytical Chemists International*, 76, 787.

Bañón, S., Costa, E., Gil, M., & Garrido, M. (2003). A comparative study of boar taint in cooked and dry-cured meat. *Meat Science*, *63*, 381–388.

Bartoň, L., Bureš, D., Kotrba, R., & Sales, J. (2014). Comparison of meat quality between eland (*Taurotragus oryx*) and cattle (*Bos taurus*) raised under similar conditions. *Meat Science*, *96*, 346–352.

Burger, J. (2002). Daily consumption of wild fish and game: exposures of high end recreationists. *International Journal of Environmental Health Research*, *12*, 343–354.

Colmenero, F. J. (2000). Relevant factors in strategies for fat reduction in meat products. *Trends in Food Science & Technology*, *11*, 56–66.

Dannenberger, D., Nuernberg, G., Nuernberg, K., & Hagemann, E. (2013). The effects of gender, age and region on macro- and micronutrient contents and fatty acid profiles in the muscles of roe deer and wild boar in Mecklenburg-Western Pomerania (Germany). *Meat Science*, *94*, 39–46.

Department of Agriculture, Forestry and Fisheries (DAFF). (2013). *Abstract of Agricultural Statistics 2013.* Compiled by Directorate Statistics and Economic Analysis. Pretoria, South Africa: Department of Agriculture, Forestry and Fisheries. Retrieved from www.nda.agric.za/docs/statsinfo/Abstract2013.xlsx.

Dry, G. (2010). Commercial Wildlife Ranching's Contribution to the Green Economy. Retrieved from http://www.sawma.co.za/images/Dry_Gert_Full_paper.pdf.

Dungait, J. A. J., Docherty, G., Straker, V., & Evershed, R. P. (2010). Seasonal variations in bulk tissue, fatty acid and monosaccharide $\delta^{13}C$ values of leaves from mesotrophic grassland plant communities under different grazing managements. *Phytochemistry*, *71*, 415–28.

Enser, M., Hallett, K., Hewitt, B., Fursey, G. A. J., & Wood, J. D. (1996). Fatty acid content and composition of English beef, lamb and pork at retail. *Meat Science*, *42*, 443–456.

Fernandes, V. R. T., Souza Franco, M. L. R., Mikcha, J. M. G., de Souza, V. L. F., Gasparino, E., Coutinho, M. E., … Del Vesco, A. P. (2014). Yacare caiman (*Caiman yacare*) trim hamburger and sausage subjected to different smoking techniques. *Journal of the Science of Food and Agriculture*, *94*, 468–72. doi:10.1002/jsfa.6270

Folch, J., Lees, M., & Sloane-Stanley, G. H. S. (1957). A simple method for the isolation and purification of total lipids from animal tissues. *Journal of Biological Chemistry*, *226*, 495–509.

Font-i-Furnols, M., & Guerrero, L. (2014). Consumer preference, behavior and perception about meat and meat products: an overview. *Meat Science*, *98*, 361–71.

Food and Agriculture Organization of the United Nations/World Health Organization (FAO/WHO). (2014). *Multicriteria-based ranking for risk management of food-borne parasites. Microbiological Risk Assessment Series No. 23*. Rome, www.fao.org/3/a-i3649e.pdf\nfiles/540/a-i3649e.pdf.

Gandemer, G. (2002). Lipids in muscles and adipose tissues, changes during processing and sensory properties of meat products. *Meat Science*, *62*, 309–321.

Girolami, A., Napolitano, F., Faraone, D., Di Bello, G., & Braghieri, A. (2014). Image analysis with the computer vision system and the consumer test in evaluating the appearance of Lucanian dry sausage. *Meat Science*, *96*, 610–6.

Hoffman, L. C. (2008). The yield and nutritional value of meat from African ungulates, camelidae, rodents, ratites and reptiles. *Meat Science*, *80*, 94–100.

Hoffman, L. C., & Cawthorn, D.–M. (2012). What is the role and contribution of meat from wildlife in providing high quality protein for consumption? *Animal Frontiers, 2*, 40–53.

Hoffman, L. C., & Sales, J. (2007). Physical and chemical quality characteristics of warthog (*Phacochoerus africanus*) meat. *Livestock Research for Rural Development*, *19,* Article 153. Retrieved from http://www.lrrd.org/lrrd19/10/hoff19153.htm.

Hoffman, L. C., Jones, M., Muller, M., Joubert, E., & Sadie, A. (2013). Lipid and protein stability and sensory evaluation of ostrich (*Struthio camelus*) droëwors with the addition of rooibos tea extract (*Aspalathus linearis*) as a natural antioxidant. *Meat Science, 96*, 1289–1296.

Hoffman, L. C., Kroucamp, M., & Manley, M. (2007a). Meat quality characteristics of springbok (*Antidorcas marsupialis*). 1: Physical attributes of springbok meat as influenced by age, gender and production region. *Meat Science*, *76*, 755–761.

Hoffman, L. C., Kroucamp, M., & Manley, M. (2007b). Meat quality characteristics of springbok (*Antidorcas marsupialis*). 2: Chemical composition of springbok meat as influenced by age, gender and production region. *Meat Science*, *76*, 762–767.

Hoffman, L. C., Mostert, A. C., Kidd, M., & Laubscher, L. L. (2009). Meat quality of kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*): Carcass yield, physical quality and chemical composition of kudu and impala *Longissimus dorsi* muscle as affected by gender and age. *Meat Science*, *83*, 788–95.

Hoffman, L. C., Muller, M., Schutte, D. W., & Crafford, K. (2004). The retail of South African game meat : current trade and marketing trends. *South African Journal of Wildlife Research*, *34*, 123–134.

Hoffman, L. C., Muller, M., Schutte, D. W., Calitz, F. J., & Crafford, K. (2005). Consumer expectations, perceptions and purchasing of South African game meat. *South African Journal of Wildlife Research*, *35*, 33–42.

Hoffman, L. C., Smit, K., & Muller, N. (2008). Chemical characteristics of blesbok (*Damaliscus dorcas phillipsi*) meat. *Journal of Food Composition and Analysis*, *21*, 315–319.

Hoffman, L., Smit, K., & Muller, N. (2010). Chemical characteristics of red hartebeest (*Alcelaphus buselaphus caama*) meat. *South African Journal of Animal Science*, *40*, 221–228.

Jenkins, T. C. (1993). Lipid metabolism in the rumen. *Journal of Dairy Science*, *76*, 3851–3863. doi:10.1016/0079-6832(78)90004-6

Kjällstrand, J., & Petersson, G. (2001). Phenolic compounds in wood smoke. *The Science of the Total Environment, 277*, 69–75.

Klingenberg, I. L., Knabe, D. A., & Smith, S. B. (1995). Lipid metabolism in pigs fed beef tallow or high-oleic acid sunflower oil. *Comparative Biochemistry and Physiology - Part B: Biochemistry and Molecular Biology, 110*, 183-192.

Koster, J. M., Hodgen, J. J., Venegas, M. D., & Copeland, T. J. (2010). Is meat flavor a factor in hunters' prey choice decisions? *Human Nature*, *21*, 219–242.

Koval, M. H., & Mertig, A. G. (2004). Attitudes of the Michigan public and wildlife agency personnel toward lethal wildlife management. *Wildlife Society Bulletin*, *32*, 232–243.

Lawless, H. T., & Heymann, H. (2010). *Sensory evaluation of food: Principals and practises* (2nd ed.). New York, USA: Chapman & Hall.

Lee, C. M., Trevino, B. & Chaiyawat, M. (1996). A simple and rapid solvent extraction method for determining total lipids in fish tissue. *Journal of AOAC International, 79*, 487–492.

Lindahl, G., Lundström, K., & Tornberg, E. (2001). Contribution of pigment content, myoglobin forms and internal reflectance to the colour of pork loin and ham from pure breed pigs. *Meat Science*, *59*, 141–151.

Lindsey, P. A., Havemann, C. P., Lines, R. M., Price, A. E., Retief, T. A., Rhebergen, T., … Romañach, S. S. (2013). Benefits of wildlife-based land uses on private lands in Namibia and limitations affecting their development. *Oryx*, *47*, 41–53.

Ljung, P. E., Riley, S. J., Heberlein, T. A., & Ericsson, G. (2012). Eat prey and love: Game-meat consumption and attitudes toward hunting. *Wildlife Society Bulletin*, *36*, 669–675.

Macmillan, D. C., & Phillip, S. (2008). Consumptive and non-consumptive values of wild mammals in Britain. *Mammal Review*, *38*, 189–204.

Marchiori, A., & Felício, P. (2003). Quality of wild boar meat and commercial pork. *Scientia Agricola*, *60*, 17–211–5.

Mostert, R., & Hoffman, L. C. (2007). Effect of gender on the meat quality characteristics and chemical composition of kudu (*Tragelaphus strepsiceros*), an African antelope species. *Food Chemistry*, *104*, 565–570.

Neethling, J., Britz, T. J., & Hoffman, L. C. (2014). Impact of season on the fatty acid profiles of male and female blesbok (*Damaliscus pygargus phillipsi*) muscles. *Meat Science*, *98*, 599–606.

Nyafu, K. (2009). *Warthog as an introduced species in the Eastern Cape*. Unpublished MSc Thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

Olssen, V., & Pickova, J. (2005). The influence of production systems on meat quality, with emphasis on pork. *Ambio, 34*, 338–343.

Pieterse, E. (2006). *Effects of increased slaughter weight of pigs on pork production*. Unpublished PhD Thesis, Stellenbosch University, Stellenbosch, South Africa. Retrieved from scholar.sun.ac.za.

Pietrasik, Z. (1999). Effect of content of protein, fat and modified starch on binding textural characteristics, and colour of comminuted scalded sausages. *Meat Science*, *51*, 17–25.

Pozio, E. (2007). World distribution of *Trichinella* spp. infections in animals and humans. *Veterinary Parasitology, 149*, 3–21.

Radder, L., & Le Roux, R. (2005). Factors affecting food choice in relation to venison: A South African example. *Meat Science*, *71*, 583–9.

Rødbotten, M., Kubberød, E., Lea, P., & Ueland, Ø. (2004). A sensory map of the meat universe. Sensory profile of meat from 15 species. *Meat Science*, *68*, 137–44.

Samples, S., Pickova, J., & Wiklund, E. (2004). Fatty acids, antioxidants and oxidation stability of processed reindeer meat. *Meat Science, 67*, 523–532.

Schoon, K. (2012). *Effect of cottonseed oilcake meal on ostrich growth performance, meat chemical composition and sensory attributes*. MSc Thesis, Stellenbosch University, Stellenbosch, South Africa.

Sebranek, J. G., & Bacus, J. M. (2007). Cured meat products without direct addition of nitrate or nitrite: What are the issues? *Meat Science, 77*, 136–147.

Skewes, O., Morales, R., González, F., Lui, J., Hofbauer, P., & Paulsen, P. (2008). Carcass and meat quality traits of wild boar (*Sus scrofa*) with 2*n*= 36 karyotype compared to those of phenotypically similar crossbreeds (2*n*= 37 and 2*n*=38) raised under same farming conditions. 1: Carcass quantity and meat dressing. *Meat Science, 80*, 1200–1204.

Somers, M. J. (1992). *The implications of social structure for conservation and control of a warthog Phacochoerus aethiopicus population in the Andries Vosloo Kudu Reserve, Eastern Cape province*. MSc Thesis, University of Pretoria, Pretoria, South Africa.

Spear, D., & Chown, S. L. (2008). Taxonomic homogenization in ungulates: patterns and mechanisms at local and global scales. *Journal of Biogeography, 35*, 1962–1975.

StatSoft, Inc. (2013). STATISTICA (data analysis software system), version 12. www.statsoft.com.

Stolte, M., Odening, K., Quandt, S., Bengis, R. G., & Bockhardt, I. (1998). *Sarcocystis dubeyella* n. sp. and *Sarcocystis phacochoeri* n. sp. (Protozoa: Sarcocystidae) from the warthog (*Phacochoerus aethiopicus*) in South Africa. *Journal of Eukaryotic Microbiology, 45*,101–104.

Swanepoel, M., Leslie, A. J., & Hoffman, L. C. (2014). The influence of season and sex on the carcass yield of common warthog (*Phacochoerus africanus*). *South African Journal of Wildlife Research*, *2000*, 179–188.

Tyburcy, A., & Kozyra, D. (2010). Effects of composite surface coating and pre-drying on the properties of kabanosy dry sausage. *Meat Science, 86*, 405–410.

Valencak, T., & Gamsjäger, L. (2014). Lipids in tissues of wild game : Overall excellent fatty acid composition, even better in free- ranging individuals. In P. Paulsen, A. Bauer, & F. J. M. Smulders (Eds.), *Trends in Game Meat Hygiene* (pp. 335–344). Wageningen, Germany: Wageningen Academic Publishers.

Van Schalkwyk, D. L., & Hoffman, L. C. (2010). *Guidelines for the Harvesting of Game for Meat Export*. Windhoek, Namibia: Printech.

Van Schalkwyk, D. L., McMillin, K. W., Booyse, M., Witthuhn, R. C., & Hoffman, L. C. (2011). Physico-chemical, microbiological, textural and sensory attributes of matured game salami produced from springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*), kudu (*Tragelaphus strepsiceros*) and zebra (*Equus burchelli*) harvested in Namibia. *Meat Science*, *88*, 36–44.

Van Schalkwyk, D. L., McMillin, K. W., Witthuhn, R. C., & Hoffman, L. C. (2010). The contribution of wildlife to sustainable natural resource utilization in Namibia: A review. *Sustainability*, *2*, 3479–3499.

Van Wyk, I. C., & Boomker, J. (2011). Parasites of South African wildlife. XVIV. The prevalence of helminths in some common antelopes, warthogs and a bushpig in the Limpopo province, South Africa. *Onderstepoort Journal of Veterinary Research, 78*, 1–11.

Van Zyl, L., & Ferreira, A. V. (2004). Physical and chemical carcass composition of springbok (*Antidorcas marsupialis),* blesbok (*Damaliscus dorcas phillipsi*) and impala (*Aepyceros melampus*). *Small Ruminent Research*, *53*, 103–109.

Warren, R. (2011). *A spending model for biltong hunters*. Unpublished PhD Thesis, North West University, Potchefstroom, South Africa.

Warris, P. (2000). *Meat Science*. Oxon, USA: CAB Publishing.

Wood, J. D., Enser, M., Fisher, A. V, Nute, G. R., Sheard, P. R., Richardson, R. I., … Whittington, F. M. (2008). Fat deposition, fatty acid composition and meat quality: A review. *Meat Science*, *78*, 343–58.

Wood, J. D., Nute, G. R., Richardson, R. I., Whittington, F. M., Southwood, O., Plastow, G., … Chang, K. C. (2004). Effects of breed, diet and muscle on fat deposition and eating quality in pigs. *Meat Science*, *67*, 651–67.

Chapter 10
Warthog management

1 Wildlife management

Wildlife management strategies attempt to find a balance between human and wildlife interactions. It has become an increasingly evolving science as humans are increasingly encroaching upon wildlife habitat and resource, which heightens the potential of human-wildlife conflict situations. These conflict situations may arise from wildlife causing damage to crops, fields, pasture and natural veld, acting as carriers of animal and zoonotic diseases, invading residential areas, interacting with other animal species, damaging infrastructure and/or injuring humans (Fall & Jackson, 2002, Riley et al., 2003). Here, wildlife management aims to mitigate conflicts typically through the use or combination of lethal and non-lethal methods. However, the lethal control has been suggested as the most effective method for vertebrate taxa (Dolbeer, 1998).

Agricultural producers are regularly in conflict with wildlife that they perceive to threaten their livelihoods (Madden, 2004), and may respond by protecting crops or vulnerable livestock through killing and trapping problem species or transforming habitat to discourage them (Treves, Wallace, Naughton-Treves, & Morales, 2006). However, because farmers recognize that wildlife has a social and economic value, they may simultaneously promote wildlife populations on their farm while trying to mitigate the damages caused (Conover, 1998). Warthogs are recognized as agricultural pests in their natural range; they are responsible for financial losses through crop-raiding or by damaging infrastructure (Mason, 1982, Somers, 1992, Vercammen & Mason, 1993). Both the Northern Cape and Free State provinces are important agricultural producers, utilizing the majority of available land for farming purposes. The introduced common warthog is therefore part of a unique paradigm where a wildlife species can be considered, and subsequently managed, as either a damage-causing or valuable wildlife species (Swanepoel, Leslie, & Hoffman, 2016 a, Chapter 4). This conflicting approach to management may result in unethical and unsustainable control practices with undesirable outcomes for both farmers and warthogs. Hunting as an informed management strategy based on scientific principles has been suggested for the successful management of warthog populations and mitigation of damages, whilst gaining financial and/or other benefits.

1.1 Hunting

Hunting is advocated as the most effective control strategy for feral pigs (*Sus scrofa*) (Geisser & Reyer, 2004). However, as mentioned in Chapter 2, hunting is only effective if it is applied consistently across succeeding seasons, as opportunistic and recreational hunting is often predictable and biased, with animals learning to detect and elude hunters. Festa-Bianchet (2008) advocated that hunting as an artificial management approach should attempt to mimic natural mortality, which requires a sound understanding of a species' population dynamics and interaction with the environment. Environmental conditions account for the majority of mortalities among warthog populations, while humans can be considered as a major predator of warthogs for meat and trophy hunting (Caro, 2005, Wilfred, 2012) and damage reprisal. Piglets and juveniles (< 1 year) are particularly vulnerable to adverse environmental conditions, (animal) predation and disease, which may result in survival rates < 50% (Mason, 1982). Somers (1992) found an estimated 55% of mortalities among juveniles due to the flooding of burrows during heavy rains. As mentioned in Chapter 2, Somers and Penzhorn (1992) found predation to be a minor contributor to warthog mortality in the Andries Vosloo Kudu Reserve (AVKR), where the leopard *(Panthera pardus)* was the only major predator present, while the presence of lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) did not affect warthog population growth in Addo Elephant National Park but did impact on the population's age structure (Mgqatsa, 2010). Warthogs also make a small contribution (9.4–13.3%) to the diet of the black backed jackal (*Canis mesomelas*) in the Great Fish River Reserve Complex (GFRRC) where larger predators are absent (Do Linh San, Malongwe, Fike, Somers, & Walters, 2009). Therefore, in addition to environmental conditions, natural mortalities among warthogs depend on the presence/absence of predators and diseases that cause warthog mortalities (Chapter 3).

Consequently, it is suggested that hunters focus their efforts on certain cohorts whilst taking environmental conditions into account (season, drought, optimal conditions) and alter the management approach accordingly. Control strategies applied to warthog populations may vary depending on the management goals. Large scale culling of animals aims to drastically reduce population numbers, while not necessarily utilizing the animals, while harvesting aims to hunt animals for meat production for the commercial market. Culling has no bias towards age or sex, while harvesting and recreational hunting is focusses on the offtake of certain groups or individuals – particularly the trophy hunting industry focuses on adult males. Large culling operations to reduce population numbers is a common practice on reserves or game farms.

Warthogs have an economic potential in terms of recreational and trophy hunting, eco-tourism and meat production but any proposed offtake strategy has to take into account species' population dynamics and interaction with the environment. Somers (1997) found warthog populations in the AVKR (currently part of the Greater Fish River Reserve [GFRR]), vulnerable to extinction even with no harvesting practices applied through a simulation program. Martin, Caro, and Borgerhoff-Mulder (2012) found warthog populations in a protected reserve in Tanzania to be disproportionately affected by illegal hunting which resulted in a drastic reduction in population number. It has also been suggested that the extinction of the Cape warthog (*Phacochoerus aethiopicus*) is in part attributable to the advancement of white settlers and bulk-grazing domestic livestock, while the introduction of firearms notably reduced the abundance of wildlife populations and altered their distribution in southern Africa (Bryden, 1893). However, some nature reserves implemented culling as a method to control introduced warthog populations but the species remained numerous and abundant within these reserves despite these control measures (Chapter 2), and the introduced warthog is still abundant in the GFRR and on adjacent lands despite their suggested vulnerability to extinction (Nyafu, 2009). In addition, their potential to increase annually vary but can be as high as 40–45% under favourable conditions (for example, absence from predators, access to water and burrows, sufficient fodder), such as when introduced to a protected area without predators (Somers & Penzhorn, 1992, Somers, 1992). However, higher population growth rates have been recorded. During the 15 years since 43 warthog were introduced in Tussen die Riviere Nature Reserve (TRNR) in the Free State Province, a protected area with no large predators, the population grew by an average of 62.6% annually, with the highest growth rates recorded between 83 and 106% in years 8 to 11 after introduction (Swanepoel, Schulze, Cumming, in press., Chapter 2). This could infer that simulation models might be inaccurate in predicting population growth rates, as available data indicates that introduced common warthogs are a low-risk extinction species.

As mentioned, hunting pressure and strategy may possibly contribute to warthog dispersal and spread, and alter behaviour patterns (Chapter 2) which could confound the problem of hunting strategies and warthog occurrence. Removing adults from a species with age and sex structured populations could affect life history traits such as reproduction and dispersal. Feral pigs are able to accelerate their life-history if there is a marked increased mortality among individuals of reproductive age achieved by timing the onset of oestrus, decreasing the length of gestation and juvenile females partitioning in reproduction (Gamelon et al., 2011, Hanson et al., 2009, Servanty et al., 2011). In excessively hunted black-backed jackal populations the removal of alpha females induces lesser females to income oestrus, resulting in increased pack fertility and population numbers, while hunting may also cause territorial breakdown in this species (Du Plessis, Avenant, & Waal, 2015). As mentioned in Chapter 2, hunters could focus their efforts on piglets and juveniles, and sows in general, for effective population reduction and control, but this might be difficult as younger individuals are smaller and less conspicuous, form smaller targets and generally illicit sympathy from hunters (Festa-Bianchet, 2008, Keuling et al., 2013). In addition, hunters might tend to cull adult sows and boars as they provide heavier carcasses and higher dress out percentages (Swanepoel, Leslie, Hoffman, 2014, Chapter 5).

Combining different hunting methods such as hunting for population control and for game meat production, might allow for wildlife management approaches to integrate ecological and human interests in wildlife management, and encourage sustainable wildlife utilization and responsible management of damage-causing species within the national regulation framework. Cromsigt et al.

(2013) suggested the novel approach of ‘hunting for fear’, where hunting events aim to elicit a behavioural response in pest animal populations to avoid areas of high human-wildlife conflict. The use of hunting for fear has had unsatisfying results in the attempt to manage feral pig populations in South Africa (Hoffman, L. C., pers. comm., 2015), where they are considered as Category 1 b invasive species defined, as “invasive species that require control by means of an invasive species management programme” (Department of Environmental Affairs [DEA], 2013). Warthogs have increased secretive, vigilant and avoidance behaviour towards humans/vehicles in areas where they are hunted (Chapter 6, Caro, 2005), while they have also been observed to avoid “new” structures or objects on agricultural properties in the Free State province, requiring periods of habituation before “accepting” the change (Unpublished data). During this study, the research team investigated the behaviour patterns and activities of introduced warthogs on a mixed cattle and game farm with the use of camera traps (Cuddeback Attack® IR, Model 1156). The cameras were installed on trees where they fitted the desired parameters (height, location) or on self-erected steel rods at other observation points as required (water and feeding points, holes in fences). The steel rods were however erected close to trees or bushes to provide some ‘camouflage’, and the camera trap models used was chosen for their infra-red flash as to not startle animals when they are photographed. Although the team expected the wild animals to be wary of the cameras at the beginning of the study, it was interesting to note that some animals such as porcupines (*Hystrix africaeaustralis*) and aardvark (*Orycteropus afer*) took almost no notice of the cameras upon encounter, while the warthogs were photo- and/or video-graphed to stop-stare as they approached the cameras, or fled upon detection (photo- and/or video-graphed). This behaviour was observed throughout the study period of ±24 months, while warthogs that appear to take no notice of cameras were established with relative certainty to be the same warthogs previously observed with the cameras e.g. they had become habituated. The team also observed similar behaviour when the environment was altered by introducing novel items such as feeding troughs. This suggests that the warthog populations, which were known to be subjected to hunting, displayed increased vigilant behaviour opposed to other species such as porcupines and aardvark which are typically not hunted in the area. Additionally, Shortridge (1934) reported that warthogs become increasingly nocturnal amidst heavy human persecution.

Schlageter and Haag-Wackernagel (2011) suggested that wild boars respond very cautiously to changes in their habitat, but there is no evidence of deterrence from neophobia (defined as the extreme or irrational fear or dislike of anything new, novel, or unfamiliar), while the use of repellents and deterrents to protect crops are effective for only short periods of time as feral pigs become habituated to these methods. There has been no research regarding deterrence from neophobia as a potential management strategy for warthogs, but it might have limited impact as warthogs reportedly have poor eyesight (Estes, 1995), and as they appear to also become habituated.

1.2 Baiting

Baiting stations and permanent water points serve as opportunistic stations to observe animal behaviour and allow for planning of culling strategies. However, baiting or feeding is not proposed as a management method as it could alter long term population dynamics (Bieber & Ruf, 2005), and increase population growth and survival in feral pig populations despite limiting environmental factors being present (Frackowiak, Gorczyca, Merta, & Wojciuch-Ploskonka, 2013, Oja, Kaasik, & Valdmann, 2014). In addition, feeding and baiting has the potential to increase damages and/or additional negative impacts from feral pigs (Geisser & Reyer, 2004). The use of baited traps to capture and retain feral pigs for translocation or euthanasia has been applied as a singular control method or in combination with other methods. There have been reports of farmers' using traps to catch warthog in South Africa (Swanepoel et al., 2016 a, Chapter 4) but it is not known whether this method is effective in terms of population control and/or damage mitigation, while trapping is labour intensive, time consuming, expensive and biased towards certain cohorts, and animals may become trap wary over time (Choquenot, Kilgour, & Lukins, 1993, Hanson et al., 2009, Williams, Holtfreter, Ditchkoff, & Grand, 2011). There use of traps, and translocation in general, also poses the risk of introducing/carrying novel pests and pathogens. For example, an ixodid tick (*Rhipicephalus gertrudae*) was recorded for the first time on warthogs among introduced populations in the Free State province (Matthee, Swanepoel, Van der Mescht, Leslie, & Hoffman, 2013, Addendum A). It has not been established whether there have been events of introduced warthogs acting as vectors of animals and human diseases in South Africa, although there was an incidence of a farmer obtaining a fatal case of Rift Valley fever (RVF) in the Northern Cape province which was suspected to be from the handling of a warthog carcass hunted on the respective farmer's property (Paweska, 2014).

It was speculated in Chapter 3 on the possibility of introduced warthogs extending the prevalence and incidence of transmission of diseases associated with warthogs in South Africa. Since warthogs are not contained with standard fencing on agricultural lands, they are therefore considered a 'free-roaming' species, and it is suggested that future research efforts should focus on the pests and pathogens associated with warthogs, and the possibility of warthogs acting as a threat to animal and human health in South Africa. It was noted that the parasites of warthogs that appear on a multi-criteria based ranking list of the most important food-borne parasites that pose a risk to humans are *E. granulosus, Trichinella* spp., and *Sarcocystis* spp. (Food and Agriculture Organization of the United Nations and the World Health Organization [FAO/WHO], 2014), which are transmitted to humans when raw or undercooked meat from infected animals is ingested. However, there is a lack of documented cases of this occurring in southern Africa. It is likely that zoonotic infections from warthog-associated parasites are underreported or misdiagnosed, or the role of warthogs as the source of infection is underappreciated in people who regularly consume bushmeat or meat from rural animals. Alternatively, it is suggested that the majority of warthogs are harvested from outside of known zoonotic distribution ranges, and that potential zoonoses are effectively controlled through current disease management programs and control zones (Chapter 3).

Poisoned baits have proved to be very effective for controlling feral pigs in Australia (Hone & Stone, 1989, Hone, 2002) but poisoning wildlife is illegal in many countries across the globe due to public sentiment and the associated environmental risks. The use of poison for control of wildlife often has significant adverse impacts on non-targeted species, and is therefore heavily opposed by conservation authorities, but this has not curbed the prevalence of this method of control (Guitart et al., 2010, Chaudhry, Ogada, Malik, Virani, & Giovanni, 2012). Although it is illegal to poison wildlife in South Africa it is still widely practised for damage animal control and bushmeat production using pesticides (Ogada, 2014). Carbofuran, a highly toxic carbamate pesticide, is the most commonly used poison in Africa for wildlife species, including 'nuisance' warthogs. Unfortunately, there is limited data available on the use and effect of poison on wildlife populations other than carnivores and scavenging species in South Africa. Considering the adverse effect on wildlife species in general, it is suggested that the use of poison in South Africa is further investigated to determine the extent of use, and impact on wildlife in general, but also targeted species. The use of poison is not considered an ethical or practical method to control wildlife species, and should be discouraged among agricultural producers and rural communities.

1.3 Alternative methods

Non-lethal control methods to control wildlife populations or mitigate the associated damages have become increasingly popular due to public scrutiny of lethal methods (Reiter, Brunson, & Schmidt, 1999) but are usually costly, labour intensive and only effective on certain species or populations. Fencing is a common tool used to manage feral pig movement (Hone & Atkinson, 1983) and there are different types of simple fences with varying degrees of effectivity, including the use of electric fencing. Electrical fencing had been hugely successful in managing the movements of black-backed jackals (*C. mesomelas*) and caracals (*C. caracal*) in South Africa (Heard & Stephenson, 1987), but the results from Chapter 4 indicate that electric fencing has not been able to contain or exclude warthogs from agricultural properties, while the damage done to fences negatively affected farmers' perceptions and management of warthogs. The use of electric fences may therefore be ineffective to control warthog movement or mitigate associated damages, including damage to fences, and alternative suggestions have been made with regards to fencing damages.

However, the evolution of the game farming industry is coupled with the use of fencing (and electric fences) to demarcate boundaries between farms with different primary types of land use (e.g. domestic stock, game animals, crops) (Swanepoel, Leslie, & Hoffman, 2016, Chapter, 4) which indicates that the use of fencing will not necessarily accommodate wildlife management ideals. However, since South Africa substantially benefits from the production and utilization of wildlife species, it is suggested that increased research efforts be conducted on the use of fencing in South Africa, as fencing has important ecological, financial and social implications (Lindsey, Masterson, Beck, & Romañach, 2012), and the construction of fences for wildlife management should consider all the possible negative impacts on the ecosystem and its inhabitants.

Some alternative ideas for managing warthogs and/or their impacts suggested by farmers include the use of reinforced fences, permanent through-ways in fences through which warthogs can move, and baited cage traps to capture warthogs (Swanepoel et al. 2016, Chapter 4). Bonnington, Grainger, Dangerfield, & Fanning (2009) found warthog movement was restricted by a two meter high fence with eight electrical wires, spaced 25 cm apart with the lowest strand at 50 cm above ground level. The only species observed to cross the fence were dik-dik (*Madoqua* spp), duikers (*Cephalophus* spp. and *Sylvicapra grimmia*), baboon (*Papio* spp.) and bushpig (*P. larvatus*). Schumann et al. (2006) tested the use of swing gates in Namibia and found that warthogs, porcupines (*Hystrix africaeaustralis*) and aardvark (*Orycteropus afer*) readily used these gates while predators tended to avoid them. It was not determined whether small livestock or game animals could also move through these through-ways, which requires further investigation as Weise, Wessels, Munro, and Solberg (2014) found that car tyres in fences were used by wildlife species, including small and large carnivores, as 'open' passageways (Figure 1). The installation of tyres was cost effective and significantly reduced fence maintenance costs, allowing certain species to permeate land-scape segregating wildlife fences. Warthogs have been observed to use the swing gates in fences to transverse fences (Figure 2). Other agricultural producers have been found to also employ the use of tyres in boundary fences as a method to allow smaller mammal movement between properties (Figure 3), which is encouraging as this could indicate that producers are becoming more willing to facilitate conservation efforts, although education efforts should attempt to provide them with specifications regarding the installation of such structures. In addition, a long term study investigating the possibility of predators 'learning' to use 'closed' passageways still needs to be conducted as this could be an ineffective strategy to prevent their access to domestic and game animals.

Figure 21: The car tyre in fence to facilitate wildlife movement as constructed by Weise, Wessels, Munro, and Solberg (2014).

Figure 22: A warthog using a swing gate to transverse the fence.

Figure 23: The use of car tyres in fences to facilitate wildlife movement.

1.4 Hunting for meat production

Assigning a monetary value to a species has proved to increase purposeful management efforts towards a species and its habitat (Festa-Bianchet, 2003). Determining the monetary value of the common warthog includes its value as a species for hunting, and the income generated from products (meat, offal, tusks, hide). Warthogs have the potential as a game animal for meat production as determined in this study (Swanepoel, Leslie, & Hoffman, 2014, Chapter 5–7), indicating that warthogs have a high dressing percentage, low total intramuscular lipid content, high total protein and a favourable fatty acid (FA) profile, while the sensory profile of fresh warthog meat appears to be influenced by intrinsic parameters such as age (Chapter 7). However, the use of warthog meat in processed products dilutes the difference between ages as assessed by sensory evaluation (Chapter 8) , which indicates the meat can be used in processed products without compromising the associated sensory experience and consumer preference of the product (Swanepoel et al. 2016, Chapter 9)

As mentioned in Chapter 2, warthogs were the 2nd most often trophy hunted in South Africa (Professional Hunters Association of South Africa [PHASA], 2014), but it is expected that the majority of recreational and damage reprisal hunting of warthogs remain unreported. Since the consumption of game meat in part promotes the social acceptability of hunting (Ljung, Riley, Heberlein, & Ericsson, 2012), the hunting and utilization of warthogs as a game animal is therefore proposed as the most likely method to aid in the management of warthog populations. Purposeful wildlife management produces game meat for local consumption with additional financial benefits. In addition, the utilization of the meat in processed products is could broaden the scope of wildlife utilization and game meat consumption, while presenting consumers with the option of healthier meat products.

The potential to benefit from wildlife has proved to serve as an incentive for South African farmers and land-owners to control and conserve wildlife and areas of natural habitat. Human consumption of an introduced species has been considered as a means of control, but it has also been cautioned considering the potential undesirable consequences (Swanepoel et al., 2016, Chapter 4). However, the hunting of feral pigs has spawned a commercial market for the meat which fed back into feral pig management (Luskin, Christina, Kelley, & Potts, 2014), and replaced the overall heavily hunted native species for bushmeat production (Desbiez, Keuroghlian, Piovezan, & Bodmer, 2011). Therefore, the regulated hunting/harvesting and meat utilization is proposed as the management strategy for introduced ungulates such as warthogs (Chapter 2). However, there are many restrictions regarding the movement of warthogs and warthog products as they are associated with diseases of economic and public health importance (Chapter 3). This could impede the development of a local market, but there has been a lack of evidence that warthogs in South Africa outside of disease-controlled areas have been implicated in diseases and/or parasitic infections in humans. Therefore, it is feasible that warthog meat has the potential to become part of the formal game meat spectrum if sourced from disease free areas. However, increased disease surveillance and research efforts should include the possibility of warthogs being able to carry and transmit potentially harmful diseases, especially as warthogs are free-roaming with expanding populations. In addition, warthog meat as a game meat should be produced according to international quality and safety standards to promote its utilization globally (Bekker, Hoffman, & Jooste, 2012, Hoffman, 2015). The recommendations made by Van der Merwe, Jooste, and Hoffman (2012) as summarized in Chapter 2 include among others to improve shot placement and evisceration techniques, and reduce the risk for microbial contamination. The practise of 'shoot-on-sight' employed by some farmers to hunt warthogs (Chapter 4) is therefore not considered a hunting method that could provide warthog carcasses destined for the commercial market. The review by Hoffman (2015) provides a comprehensive overview on the safety and hygiene requirements to produce game meat in the bush.

In Swanepoel et al. (2016, Chapter 4) some farmers indicated that they considered warthogs to have value other than for meat production. These included their value as a game animal for eco-tourism and aesthetics. Aesthetics refers to the notion that farmers themselves feel warthogs contribute to the beauty of natural environment. Two farmers were of the opinion that products made from the tail, hide, or tushes may have financial value, while warthogs are also considered a charismatic species which contribute to tourist satisfaction (Maciejewski & Kerley, 2014). The alternative aspects associated with warthog value and/or enjoyment is presented in Table 1. Local markets trade in warthog ivory obtained from the tushes (formal term for tusks in this family). The tushes are sometimes kept as decorative or novelty items by hunters and farmers, and a number of interesting items are produced from the tushes for commercial and tourism markets (Figure 4). The potential to increase the utilization of warthog ivory opposed to elephant (*Loxodonta africana*) ivory has been suggested, but this avenue has not shown potential or has been further explored at present. Hunters may also request for mounts to be made from the warthogs hunted (Figure 5).

Table 27: Alternative aspects associated with warthogs of value and enjoyment.

Aspect	Example	References
Tourism	Eco-tourism	Maciejewski & Kerley (2014)
	Hunter and tourism satisfaction	Maciejewski & Kerley (2014)
	Wildlife photography	
Products	Ivory	D. Cumming (n.d.) in Vercammen & Mason (1993)
	Trophies	Wilfred (2012)
	Animal mounts	
	Tanned skins	Swanepoel et al., (2016)
Meat	Bushmeat	Martin et al. (2012)
	Meat for farm workers	Swanepoel et al. (2016)
Research	Wildlife management science	Swanepoel et al. (2016)
	Invasion science	Nyafu (2009)
	Population dynamics	Somers (1992), White (2010), White et al. (2009, 2011)
	Environmental and agricultural impacts	Nyafu (2009), Swanepoel et al. (2016)
Miscellaneous	Farmer and land owner enjoyment/appreciation	Swanepoel et al. (2016)
	Pets	C. van Niekerk, pers. comm. (2012)

Figure 24: Examples of the products produced with warthog tushes.

Figure 25: A head and shoulder mount of warthog.

2 Management implications

The common warthog (*Phacochoerus africanus*) has been classified as an alien invasive species in the Eastern Cape province of South Africa (Nyafu, 2009). However, according to Government Notice 599 National Environmental Management: Biodiversity Act (10/2004): Alien and Invasive Species List, 2014 (NEMBA), all extra-limital taxa (other than fresh-water fish) present in the Republic of South Africa are exempted from the restricted activities involving alien species in terms of section 65 (1) (NEMBA) with the effect of Notice 2 (Government Notice, 1 August 2014) (DEA, 2013). This includes the extra-limital common warthog in South Africa, which generally mean that warthogs are considered an indigenous species to the country while current regulation of activities pertaining to native and extra-limital warthogs is determined by individual provincial authorities (Table 2). However, in terms of the National Environmental Management: Biodiversity Act (10/2004): Norms and Standards for the translocation of indigenous species in South Africa (DEA, 2015), warthogs are listed among the species to which an application for exemption of permits in terms of provincial legislation may be considered. This could further complicate the management and regulation of extra-limital warthogs in South Africa, as the species is free-roaming and therefore not limited by provincial boundaries. There is still debate regarding the exact historical distribution range of the species in South Africa (Kerley & Boshoff, 2014, Boshoff, Landman, & Kerley, 2015, Chapter 2), while Bernard and Parker (2006) suggested that the most recent information on the distribution of a species in South Africa should be considered more important as reliable records of historical distribution is lacking.

Table 28: The regulations of activities pertaining to warthogs as determined by provincial authorities.

Province	Hunt/catch/kill	Importing/exporting/ translocating	Possessing/ controlling	Trading/buying/ selling
Limpopo	Require permit	Require permit	Require permit	Permit not required
North West	Require permit	Prohibited	Prohibited	Prohibited
Eastern Cape	Permit not required	Require permit	Permit not required	Permit not required
Northern Cape	Require permit	Prohibited	Prohibited	Prohibited
KwaZulu Natal	Require permit	Require permit	Permit not required	Require permit
Mpumalanga	Permit not required*	Require permit	Require permit	Require permit[#]
Free State	Permit not required**	Require permit	Permit not required	Require permit
Gauteng	Require permit	Require permit	Require permit	Require permit
Western Cape	Require permit	Prohibited	Prohibited	Prohibited

*Permission from landowner.
**If registered as game animal trader.
[#]If game animal is alive, written consent if game animal is a product.

This could imply that the species may rather be referred to and managed as a damage-causing animal, which is defined as "a wild vertebrate animal that, when interacting with humans or interfering with human activities, there is substantial proof that it a) causes losses to stock or other wild specimens, b) causes damage to cultivated trees, crops, natural flora or property, c) presents a threat to human life; or d) is present in such numbers that agricultural grazing material is materially depleted" according to the Draft Norms and Standards for the Management of Damage Causing Animals in South Africa (DEA, 2010). The control of damage causing animals requires that the necessary permits be obtained and that the control is exercised by trained persons. However, it is common practise for farmers to opportunistically kill the animals they perceive as damage-causing, which makes it difficult for authorities to regulate wildlife management as farmers might abstain from obtaining permits or notifying authorities. In addition, social and environmental factors rather than actual economic losses may drive human-wildlife conflict (HWC) among farmers in South Africa (Thorn, Green, Dalerum, Bateman, & Scott, 2012).

The control of a damage-causing wildlife species aims to regulate populations while mitigating the adverse impacts exerted by the species on the natural and agricultural environment. While the ecological impacts of the introduced common warthog have not yet been determined, the negative impacts on the agricultural environment are of concern to agricultural producers (Nyafu, 2009, Swanepoel et al., 2016, Chapter 4). An example of the damage warthogs caused to crops is given in Figure 6. The principles of wildlife management as documented in scientific literature for feral pigs (Chapter 2), provides a framework for formulating potential warthog management strategies. For warthogs, a combination of lethal and non-lethal strategies is suggested to control population numbers and mitigate damages experienced, whilst encouraging sustainable utilization and ethical management.

A fundamental aspect in developing an appropriate wildlife management strategy involves understanding the basic ecology and dynamics of the species e.g. life history traits. The vital characteristics of population dynamics including fecundity, survival, growth, maturation, recruitment, dispersal, behaviour, activity and interaction with the environment, are used to determine the sensitivity of a population to different management strategies (Gordon, Hester, & Festa-Bianchet, 2004). Therefore, wildlife management should not only focus on decreasing population numbers in HWC situations, but take the population structure dynamics into account as randomized off-taking of individuals may lead to a disruption of stable population dynamics and impact on reproduction, survival and behaviour (Festa-Bianchet, 2003), as found for feral pigs. (Gamelon et al., 2011, Hanson et al., 2009, Servanty et al., 2011)

Warthogs were introduced to habitats outside of their known natural distribution range, which largely encompasses land utilized for agricultural production. Their interaction with the environment in terms of life history traits has not been considered as a potential factor affecting population dynamics, and consequently the potential to influence suggested management strategies. It is therefore considered an important avenue for future research to investigate the overall ecology of warthogs in the introduced habitats to assist in the development of management strategies.

Figure 6: The damage caused to crop fields by the common warthog (*Phacochoerus africanus*) (Photo A. Leslie).

3 Conclusion

While hunting and utilization is proposed as the most feasible method to approach warthog management, the implementation, outcomes and hurdles associated will influence the effectiveness of this strategy in the long term. There are still avenues warranting research regarding the distribution, impacts, utilization and management of warthog populations in South Africa and this study is one of the first and most recent to address an introduced population in South Africa in terms of these aspects. This study provides encouraging avenues to explore for further research into the management of warthogs and the production of game meat.

4 References

Bekker, J. L., Hoffman, L. C., & Jooste, P. J. (2012). Wildlife-associated zoonotic diseases in some southern African countries in relation to game meat safety: A review. *The Onderstepoort Journal of Veterinary Research*, *79*, E1–E12. doi:10.4102/ojvr.v79i1.422

Bieber, C., & Ruf, T. (2005). Population dynamics in wild boar *Sus scrofa*: Ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *Journal of Applied Ecology*, *42*, 1203–1213. doi:10.1111/j.1365-2664.2005.01094.x

Bonnington, C., Grainger, M., Dangerfield, S., & Fanning, E. (2009). The influence of electric fences on large mammal movements in the Kilombero Valley, Tanzania. *African Journal of Ecology*, *48*, 280–284.

Boshoff, A., Landman, M., & Kerley, G. (2015). Filling the gaps on the maps : historical distribution patterns of some larger mammals in part of southern Africa. *Transactions of the Royal Society of South Africa*. doi:10.1080/0035919X.2015.1084066

Braga, C., Alexandre, N., Fernández-Llario, P., & Santos, P. (2010). Wild boar (*Sus scrofa*) harvesting using the espera hunting method: side effects and management implications. *European Journal of Wildlife Research*, *56*, 465–469. doi:10.1007/s10344-010-0373-1

Bryden, H. A. (1893). *Gun and camera in Southern Africa*. *Edward Stanford*. London, England: Edward Stanford. Retrieved from https://archive.org/details/guncamerainsouth00bryd.

Caro, T. M. (2005). Behavioural indicators of exploitation. *Ethology Ecology & Evolution*, *17*, 189–194. doi:10.1080/08927014.2005.9522608

Chaudhry, M. J. I., Ogada, D. L., Malik, R. N., Virani, M. Z., & Giovanni, M. D. (2012). First evidence that populations of the critically endangered Long-billed Vulture (*Gyps indicus*) in Pakistan have increased following the ban of the toxic veterinary drug diclofenac in south Asia. *Bird Conservation International*, *22*, 389–397. doi:10.1017/S0959270912000445

Choquenot, D., Kilgour, R., & Lukins, B. (1993). An evaluation of feral pig trapping. *Wildlife Research*, *20*, 15. doi:10.1071/WR9930015

Conover, M. R. (1998). Perceptions of American agricultural producers about wildlife on their farms and ranches. *Wildlife Society Bulletin*, *26*, 597–604.

Cromsigt, J. P. G. M., Kuijper, D. P. J., Adam, M., Beschta, R. L., Churski, M., Eycott, A., … West, K. (2013). Hunting for fear: innovating management of human-wildlife conflicts. *Journal of Applied Ecology*, *50*, 544–549. doi:10.1111/1365-2664.12076

Department of Environmental Affairs (DEA). (2010). National Environmental Management: Biodiversity Act 2004 (Act No. 10 of 2004). Draft norms and standards for management of damage-causing animals in South Africa. Government Gazette (33806). Retrieved from https://www.environment.gov.za/sites/default/files/gazetted_notices/nemba_draftnormsandstandards_g33806gen1084.pdf

Department of Environmental Affairs (DEA). (2013). National Environmental Management: Biodiversity Act 2004 (Act No. 10 of 2004): Alien and Invasive Species Regulations. Government Gazette (36683). doi:http://dx.doi.org/9771682584003-32963

Desbiez, J. A. L., Keuroghlian, A., Piovezan, U., & Bodmer, R. E. (2011). Invasive species and bushmeat hunting contributing to wildlife conservation: the case of feral pigs in a Neotropical wetland. *Oryx*, *45*, 78–83. doi:10.1017/S0030605310001304

Dolbeer, R. A. (1998). Population dynamics: Age foundation of wildlife damage management for the 21st century. In *Vertebrate Pest Conference Proceedings* (pp. 1–11). Costa Mesa.

Do Linh San, E., Malongwe, N. B., Fike, B., Somers, M. J., & Walters, M. (2009). A diverse autumn diet without dominant prey for opportunistic black-backed jackals *Canis mesomelas*. *Wildlife Biology in Practice*, *5*, 96–103. doi:10.2461/wbp.2009.5.10

Du Plessis, J. J., Avenant, N. L., & De Waal, H. O. (2015). Quality and quantity of the scientific information available on black-backed jackals and caracals : contributing to human – predator conflict management ? *African Journal of Wildlife* Research, *45*, 138–157.

Estes, R. D. (1995). The behaviour guide to African mammals: Including hoofed mammals, carnivores, primates. Halfway House, South Africa: Russel Friedman Books

Fall, M. W., & Jackson, W. B. (2002). The tools and techniques of wildlife management damage management – changing needs: An introduction. *International Biodeteriation and Biodegradation, 49*, 87–91.

Festa-Bianchet, M. (2003). Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. In M. Festa-Bianchet & M. Apollonio (Eds.), *Animal behavior and wildlife conservation* (pp 191–207). Washington DC, USA: Island Press.

Festa–Bianchet, M. (2008). Ecology, evolution, economics, and ungulate management. In T. E. Fulbright, & D. G. Hewitt (Eds.), *Wildlife science: Linking ecological theory and management applications* (pp. 183–202). Florida, USA: CRC, Boca Raton.

Food and Agriculture Organization of the United Nations/World Health Organization (FAO/WHO). (2014). *Multicriteria-based ranking for risk management of food-borne parasites*. *Microbiological Risk Assessment Series No. 23*. Retrieved from www.fao.org/3/a-i3649e.pdf\nfiles/540/a-i3649e.pdf.

Frackowiak, W., Gorczyca, S., Merta, D., & Wojciuch-Ploskonka, M. (2013). Factors affecting the level of damage by wild boar in farmland in north-eastern Poland. *Pest Management Science*, *69*, 362–366. doi:10.1002/ps.3368

Gaillard, J., Festa-Bianchet, M., Yoccoz, N., Loison, A., & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, *31*, 367–393. Retrieved from http://www.jstor.org/stable/221737

Gamelon, M., Besnard, A., Gaillard, J., Servanty, S., Baubet, E., Brandt, S., & Gimenez, O. (2011). High hunting pressure selects for earlier birth date: Wild boar as a case study. *Evolution*, *65*, 3100–3112. doi:10.1111/j.1558-5646.2011.01366

Geisser, H., & Reyer, H. (2004). Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. *The Journal of Wildlife Management*, *68*, 939–946.

Gordon, I. J., Hester, A. J., & Festa-Bianchet, M. (2004). Review: The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology*, *41*, 1021–1031. doi:10.1111/j.0021-8901.2004.00985.x

Guitart, R., Sachana, M., Caloni, F., Croubels, S., Vandenbroucke, V., & Berny, P. (2010). Animal poisoning in Europe. Part 3: Wildlife. *Veterinary Journal*, *183*, 260–265. doi:10.1016/j.tvjl.2009.03.033

Hanson, L. B., Mitchell, M. S., Grand, J. B., Jolley, D. B., Sparklin, B. D., & Ditchkoff, S. S. (2009). Effect of experimental manipulation on survival and recruitment of feral pigs. *Wildlife Research*, *36*, 185–191. doi:10.1071/WR08077

Heard, H., & Stephenson, A. (1987). Electrification of a fence to control the movements of black-backed jackals. *Suid Afrika Tydskrif van Natuurnavorsing*, *17*, 20–24.

Hoffman, L. C. (2015). Producing game meat to meet international hygiene and food safety requirements in the bush. In *Annual Reciprocal Meat Conference* (pp. 1–12). Auburn University in Auburn, Alabama, 16–19 June 2015.

Hoffman, L. C., Muller, M., Schutte, D. W., Calitz, F. J., & Crafford, K. (2005). Consumer expectations , perceptions and purchasing of South African game meat. *South African Journal of Wildlife Research*, *35*, 33–42.

Hone, J. (2002). Feral pigs in Namadgi National Park, Australia: Dynamics, impacts and management. *Biological Conservation*, *105*, 231–242. doi:10.1016/S0006-3207(01)00185-9

Hone, J., & Atkinson, B. (1983). Evaluation of fencing to control feral pig movement. *Australia Wildlife Research*, *10*, 499–505.

Hone, J., & Stone, C. P. (1989). A comparison and evaluation of feral pig management in two national parks. *Wildlife Society Bulletin*, *17*, 419–425. doi:10.2307/3782705

Kerley, G. I. H., & Boshoff, A. F. (2014). Letter To The Editor: The common warthog and its parasites in the Free State Province (South Africa) cannot be used to test the “enemy release” hypothesis for an introduced species: the value of reference point information for testing hypotheses of change. *African Zoology*, *49*, 169. doi:10.1080/13518040701205365

Keuling, O., Baubet, E., Duscher, A., Ebert, C., Fischer, C., Monaco, A., … Thurfjell, H. (2013). Mortality rates of wild boar *Sus scrofa* L. in central Europe. *European Journal of Wildlife Research*, *59*, 805–814. doi:10.1007/s10344-013-0733-8

Lindsey, P. A., Masterson, C. L., Beck, A. L., & Romañach, S. S. (2012). Fencing for Conservation. In M. J. Somers & M. W. Haywards (Eds.), *Fencing for Conservation: Restriction of Evolutionary Potential or a Riposte to Threatening Processes?* (pp. 215–234). New York, USA: Springer-Verlag. doi:10.1007/978-1-4614-0902-1

Ljung, P. E., Riley, S. J., Heberlein, T. A., & Ericsson, G. (2012). Eat prey and love: Game-meat consumption and attitudes toward hunting. *Wildlife Society Bulletin*, *36*, 669–675. doi:10.1002/wsb.208

Luskin, M. S., Christina, E. D., Kelley, L. C., & Potts, M. D. (2014). Modern hunting practices and wild meat trade in the oil palm plantation-dominated landscapes of Sumatra, Indonesia. *Human Ecology*, *42*, 35–45. doi:10.1007/s10745-013-9606-8

Maciejewski, K., & Kerley, G. I. H. (2014). Understanding tourists' preference for mammal species in private protected areas: is there a case for extralimital species for ecotourism? *PloS One*, *9*, e88192. doi:10.1371/journal.pone.0088192

Madden, F. (2004). Creating coexistence between humans and wildlife: global perspectives on local efforts to address human–wildlife conflict. *Human Dimensions of Wildlife*, *9*, 247–257. doi:10.1080/10871200490505675

Martin, A., Caro, T., & Borgerhoff Mulder, M. (2012). Bushmeat consumption in western Tanzania: A comparative analysis from the same ecosystem. *Tropical Conservation Sciences*, *5*, 352–364.

Mason, D. R. (1982). *Studies on the biology and ecology of the warthog Phacochoerus aethiopicus sundevalli Lönnberg, 1908 in Zululand*, *South Africa*. Dissertation, University of Pretoria, Pretoria, South Africa.

Matthee, S., Swanepoel, M., Van der Mescht, L., Leslie, A. J., & Hoffman, L. C. (2013). Ectoparasites of a non-indigenous warthog population, *Phacochoerus africanus*, in the Free State Province, South Africa. *South African Journal of Wildlife Research*, *48*, 259–265. doi:10.3377/004.048.0210

Mgqatsa, N. (2010). *Diet and population trends of warthog in the Addo Elephant National Park*. MSc thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

Nyafu, K. (2009). *Warthog as an introduced species in the Eastern Cape*. MSc thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

Ogada, D. L. (2014). The power of poison: Pesticide poisoning of Africa's wildlife. *Annals of the New York Academy of Sciences*, *1322*, 1–20. doi:10.1111/nyas.12405

Oja, R., Kaasik, A., & Valdmann, H. (2014). Winter severity or supplementary feeding—which matters more for wild boar? *Acta Theriologica*, *59*, 553–559. doi:10.1007/s13364-014-0190-0

Paweska, J. T. (2014). Rift Valley fever. In Ö. Ergönul, F. Can, M. Akova, & L. Madoff (Eds.), *Emerging infectious diseases: Clinical case studies.* London, England: Academic Press.

Professional Hunters Association of South Africa (PHASA). (2014). *Revenue from hunting tourists breaks R1 billion mark.* Retrieved from www.phasa.co.za/what-is-in-the-news/phasa-press-release/item/570-revenue-from-hunting-tourists-breaks-r1-billion-mark.html.

Reidy, M. M., Campbell, T. A., & Hewitt, D. G. (2008). Evaluation of electric fencing to inhibit feral pig movements. *Journal of Wildlife Management*, *72*, 1012–1018. doi:10.2193/2007-158

Reiter, D. K., Brunson, M. W., & Schmidt, R. H. (1999). Public attitudes toward wildlife damage management and policy. *Wildlife Society Bulletin*, *27*, 746–758.

Riley, S., Siemer, W., Decker, D., Carpenter, L., Organ, J., & Berchielli, L. (2003). Adaptive impact management: an integrative approach to wildlife management. *Human Dimensions of Wildlife*, *8*, 81–95. doi:10.1080/10871200304301

Schlageter, A., & Haag-Wackernagel, D. (2011). Effectiveness of solar blinkers as a means of crop protection from wild boar damage. *Crop Protection*, *30*, 1216–1222. doi:10.1016/j.cropro.2011.05.008

Schumann, M., Schumann, B., Dickman, A., Watson, L. H., & Marker, L. (2006). Assessing the use of swing gates in game fences as a potential non-lethal predator exclusion technique. *South African Journal of Wildlife Research*, *36*, 173–181.

Servanty, S., Gaillard, J. M., Ronchi, F., Focardi, S., Baubet, É., & Gimenez, O. (2011). Influence of harvesting pressure on demographic tactics: Implications for wildlife management. *Journal of Applied Ecology*, *48*, 835–843. doi:10.1111/j.1365-2664.2011.02017.x

Shortridge, G. C. (1934). *The mammals of South West Africa*. London, England: W. Heinemann, Ltd.

Somers, M. J. (1992). *The implications of social structure for the conservation and control of a warthog Phacochoerus aethiopicus population in the Andries Vosloo Kudu Reserve, Eastern Cape Province*. MSc Thesis, University of Pretoria, Pretoria, South Africa.

Somers, M. J. (1997). The sustainability of harvesting a warthog population: assessment of management options using simulation modelling. *South African Journal of Wildlife Research*, *27*, 37–43.

Somers, M. J., & Penzhorn, B. L. (1992). Reproduction in a reintroduced warthog population in the eastern Cape Province. *South African Journal of Wildlife Research*, *22*, 57–57. Retrieved from http://www.sabinet.co.za/abstracts/wild/wild_v22_n3_a1.html

Swanepoel, M., Leslie, A. J., & Hoffman, L. C. (2016). Farmers' perceptions of the extra-limital common warthog in the Northern Cape and Free State provinces, South Africa. *Wildlife Society Bulletin*. doi:10.1002/wsb.617.

Swanepoel, M., Leslie, A. J. & Hoffman, L. C. (2016). Comparative analyses of the chemical and sensory parameters and consumer preference of a semi-dried smoked meat product (cabanossi) produced with warthog (*Phacochoerus africanus*) and domestic pork meat. *Meat Science, 114*, 103–113. doi:10.1016/j.meatsci.2015.12.002.

Swanepoel, M., Leslie, A. J., & Hoffman, L. C. (2014). The influence of season and sex on the carcass yield of common warthog (*Phacochoerus africanus*). *South African Journal of Wildlife Research*, *44*, 179–188.

Swanepoel, M., Schulze, E., & Cumming, D. (in press.). A conservation assessment of *Phacochoerus africanus*. In M. F. Child, D. Raimondo, E. Do Linh San, L. Roxburgh & H. Davies-Mostert (Eds.), *The Red List of Mammals of South Africa, Swaziland and Lesotho*. Pretoria, South Africa: South African National Biodiversity Institute and Endangered Wildlife Trust.

Thorn, M., Green, M., Dalerum, F., Bateman, P. W., & Scott, D. M. (2012). What drives human–carnivore conflict in the North West Province of South Africa? *Biological Conservation*, *150*, 23–32. doi:10.1016/j.biocon.2012.02.017

Treves, A., Wallace, R. B., Naughton-Treves, L., & Morales, A. (2006). Co-managing human–wildlife conflicts: A review. *Human Dimensions of Wildlife*, *11*, 383–396. doi:10.1080/10871200600984265

Van der Merwe, M., Jooste, P. J., & Hoffman, L. C. (2012). Application of European standards for health and quality control of game meat on game ranches in South Africa. *Journal of the South African Veterinary Association*, *82*, 170–175. doi:10.4102/jsava.v82i3.63

Vercammen, P. & Mason, D. R. (1993). *The Warthogs* (P*hacochoerus africanus* and *P. aethiopicus*). In W. L. R. Oliver (Ed.), *Pigs, Peccaries, and Hippos: Status Survey and Conservation Action Plan* (pp. 75-84). Gland, Switzerland: IUCN/SSC Pigs and Peccaries Specialist Group. Retrieved from https://portals.iucn.org/library/efiles/edocs/1993-055.pdf.

Weise, F. J., Wessels, Q., Munro, S., & Solberg, M. (2014). Using artificial passageways to facilitate the movement of wildlife on Namibian farmland. *South African Journal of Wildlife*, *44*, 161–166.

White, A. M., & Cameron, E. Z. (2009). Communal nesting is unrelated to burrow availability in the common warthog. *Animal Behaviour*, *77*, 87–94. doi:10.1016/j.anbehav.2008.08.030

White, A. M. (2010). A pigheaded compromise: do competition and predation explain variation in warthog group size? *Behavioral Ecology*, *21*, 485–492. doi:10.1093/beheco/arq009

White, A. M., & Cameron, E. Z. (2011). Fitness consequences of maternal rearing strategies in warthogs: influence of group size and composition. *Journal of Zoology*, *285*, 77–84. doi:10.1111/j.1469-7998.2011.00816.x

Wilfred, P. (2012). Trophy hunting and trophy size in Ugalla Game Reserve, western Tanzania. *Tanzania Journal of Science*, *38*, 111–122.

Williams, B. L., Holtfreter, R. W., Ditchkoff, S. S., & Grand, J. B. (2011). Trap style influences wild pig behavior and trapping success. *The Journal of Wildlife Management*, *75*, 432–436. doi:10.1002/jwmg.64

Chapter 11
General discussion and conclusions

The common warthog (*Phacochoerus africanus*) was introduced to various game farms and reserves in the Eastern Cape, Northern Cape and the Free State provinces of South Africa. The first introductions conducted by conservation authorities were considered as a re-introduction of a locally extinct warthog species (*P. aethiopicus*), while further introductions followed for game farming and ranching purposes if the property was sufficiently fenced to enclose populations. Warthogs were able to escape enclosures and become free-roaming, establishing naturalized populations in the habitat, reproduce and disperse within the habitat, and exert negative impacts on the natural and agricultural environment (Chapter 2, 4), with the potential to act as vectors of animal and human diseases (Chapter 3). Currently they occur wide-spread in South Africa (Chapter 2) and have been classified as an invasive species in parts of South Africa considering their impacts (Nyafu, 2009). However, according to the Government Notice 599 National Environmental Management: Biodiversity Act (10/2004): Alien and Invasive Species List, 2014 (NEMBA), all extra-limital taxa (other than fresh-water fish) present in the Republic of South Africa are exempted from the restricted activities involving alien species in terms of section 65 (1) (NEMBA) with the effect of Notice 2 (Government Notice, 1 August 2014, Department of Environmental Affairs [DEA], 2014). This includes the extra-limital common warthog in South Africa, which generally mean that warthogs are considered an indigenous species to the country while current regulation of activities pertaining to native and extra-limital warthogs is determined by individual provincial authorities (Chapter 10). However, in terms of the National Environmental Management: Biodiversity Act (10/2004): Norms and Standards for the translocation of indigenous species in South Africa (DEA, 2015), warthogs are listed among the species to which an application for exemption of permits in terms of provincial legislation may be considered. This could further complicate the management and regulation of extra-limital warthogs in South Africa, as the species is free-roaming and therefore not limited by provincial boundaries.

It is therefore suggested that common warthogs may rather be referred to as a damage-causing animal according to the Draft Norms and Standards for the Management of Damage Causing Animals in South Africa (DEA, 2010) (Chapter 10). The control of damage causing animals requires that the necessary permits be obtained and that the control is exercised by trained persons, however, it is common practise for farmers to opportunistically kill the animals they perceive as damage-causing, which makes it difficult for authorities to regulate wildlife management as farmers might abstain from obtaining permits or notifying authorities.

The introduced common warthog are simultaneously considered as an agricultural pest and valuable game animal by farmers, and are hunted for damage reprisal and for financial gains through meat and trophy hunting (Swanepoel, Leslie, Hoffman, 2016, Chapter 4). The species is therefore part of a unique paradigm where a wildlife species can be considered, and subsequently managed, as either a damage-causing or valuable species. This conflicting approach to management results in unethical and unsustainable control practices with undesirable outcomes for both farmers and warthogs. Despite their potential for game meat production, they are still relatively under-utilized accordingly in South Africa. Consequently, considering the lack of available scientific literature on the quality characteristics of warthog meat, this study aimed to investigate the hunting and utilization of warthogs as a strategy to encourage management and game meat production.

The first step was to determine how introduced warthogs and their impacts are perceived by farmers and how the species are subsequently managed. Potential participants were identified in the parts of the Free State and Northern Cape provinces using the Snowball technique and interviewed during semistructured personal interviews using a standardized questionnaire through personal semi-structures interviews with farmers. Warthogs were held responsible for causing damage to aspects of the natural and agricultural environment, while livestock farmers were more negative than game farmers concerning the impacts warthogs have on the agricultural environment, but not the natural environment (Swanepoel et al., 2016, Chapter 4). Overall, farmers were increasingly negative toward warthogs as the levels of perceived damages increased. Despite this, a number of farmers regarded and utilized the species as a game animal, while the majority hunted and utilized warthogs for meat consumption. Nonlethal management was practiced by only 7% of farmers. Most were of the opinion that warthogs have indirectly resulted in livestock and game animal losses – the main reason being the damage caused to fences that allow predators to gain access to these animals. The majority (80%) indicated that they would be more likely to utilize the meat if presented with information on its nutritional profile. This provided the baseline for the study to conduct a thorough investigation into the parameters and quality characteristics of warthog meat, and its potential to be produced for fresh game meat consumption and use in processed game meat products.

There was also concern among farmers that warthogs could be responsible for introducing and transmitting pests and parasites to animals and humans, while there has also been general concern that consumption of warthog meat could cause diseases or parasitic infections in humans. Warthogs are associated with a number of important animal and zoonotic diseases, such as African Swine Fever (ASF) and bovine tuberculosis (bTB), with the potential to act as a wild reservoir. This raises serious concerns as the species are not restricted by standard fencing and move freely among natural and agricultural lands, with their distribution range expanding across South Africa (Chapter 3). It was therefor considered of value to investigate the ectoparasites of an introduced warthog population in order to partly elucidate on their potential to act as vectors of diseases. The study made use of the warthogs culled during three seasons for the subsequent investigation of warthog yields and meat characteristics (Addendum A) to collect ectoparasites. In general, it was found that parasite species richness in the introduced host population was low, which could support the parasite release hypothesis (Matthee, Swanepoel, Van der Mescht, Leslie, & Hoffman, 2013, Addendum A), which states that the absence of native enemies aids exotic species in distributing and becoming abundant. In addition, the study found the first record of the tick *Rhipicephalus gertrudae* on warthogs in South Africa to date, while the low abundance of *R. simus* was attributed to the fact that the study area largely fell outside the ticks' preferred distribution range. These results may prematurely suggest that introduced warthogs can alter the distribution of parasites, and/or act as host to parasites not previously associated with warthogs. The free-ranging and extra-limital warthogs therefore pose a risk as potential disease vectors, which requires future research efforts especially since the expansion of game farming industry often result in high stocking densities, close proximity of different animal species and frequent animal transportation (Bekker, Hoffman, & Jooste, 2012).

Although warthogs are able to carry and transmit diseases to humans, there is a lack of documented cases of this occurring in southern Africa. In addition, no warthogs culled during this study showed obvious symptoms of diseases or of being carriers of parasites potentially harmful for human consumption, albeit this was not explicitly investigated in this study. It was suggested that zoonotic infections from warthog-associated parasites are underreported or misdiagnosed, or the role of warthogs as the source of infection is underappreciated in people who regularly consume bushmeat or meat from rural animals. It was also suggested that the majority of warthogs are harvested from outside of known zoonotic distribution ranges and that potential zoonosis are effectively controlled through current disease management programs and control zones. If the latter is true then warthog meat has the potential to become part of the formal game meat spectrum if sourced from disease free areas.

If a species is to be utilized commercially, information on the yields and the factors that influence this are required to evaluate the economic feasibility for utilization. The yields of warthogs were subsequently determined as influenced by three parameters - season, age and sex, in light of promoting the species for commercial meat production in South Africa. (Swanepoel, Leslie, & Hoffman, 2014, Chapter 5). Although it was initially envisaged to include the effect of age there were to many imbalances in the samples' population to allow for this, but the study did include a short description of the data from juvenile warthogs. Season did not have a significant impact on the carcass weights and dress out percentages of adult warthogs, while males had heavier carcass weights (35.24 kg) than females (27 kg) and had a higher dress out percentage (57.14%) than females (52.14%). Male juveniles tended to have a heavier body weight (29.5kg) than female juveniles (19.3kg), but very similar dress out percentages (48.7% and 48.2%, respectively). The general carcass yield of common warthogs and other wild ungulates average around 56-66% for mature (adult) animals of both sexes, similar to the 65.5% for wild boars (*Sus scrofa*). Overall, adult warthogs had a favourable carcass yield and can therefore be utilized for commercial game meat production across hunting seasons. It was unfortunate that the imbalance of sampled populations across seasons did not allow for the inclusion of season and age as a factor, as it is known that animal maturity and environmental factors such as season can influence the physical and chemical characteristics of meat, especially in wild animals (Neethling, Hoffman, & Britz, 2013, Neethling, Britz, & Hoffman, 2014). It is suggested that future studies include these factors for investigation, as well as the influence of region in terms of origin which may also affect meat quality characteristics (Erasmus, Muller, Van der Rijst, & Hoffman, 2016). This is considered necessary with regards to warthog meat as the species is expanding its known distribution range across South Africa (Swanepoel, Schulze, & Cumming, in press., Chapter 2) and as some provinces have strict regulations in terms of hunting season.

In view of these findings, it was considered to investigate the overall quality and nutrition profile of warthog meat since the species is still under-utilized by hunters and/or the commercial sector while the majority farmers interviewed in Chapter 4 (Swanepoel et al., 2016) indicated that they would be more willing to utilize the meat if presented with information on its nutritional profile. It has been contended that game meat should be classified and marketed according to species, and possibly according to sex and season of harvesting (Rødbotten, Kubberød, Lea, & Ueland, 2004, Hoffman, Mostert, & Laubscher, 2009, Valencak, Gamsjäger, Ohrnberger, Culbert, & Ruf, 2015). In addition, the meat from wild animals has often been sold under collective terms of 'game meat' and 'venison' but it has been suggested that wild animal muscles are sold as separate muscles rather than the typical commercial cuts. The study therefore investigated the effect of sex and age on the meat quality characteristics of six different skeletal muscles (Chapter 6). Again, although it was envisaged to investigate the effect of season and age on meat characteristics, the imbalances in sampled populations did not allow for this, while a description of the data from juveniles were provided (Chapter 6). As there were differences found in the yields and physical characteristics of the six muscles between sexes, the study concluded that warthog meat should be marketed and labelled as whole muscle cuts. However, the differences in the chemical profile between sexes and among muscles are considered negligible in terms of its nutrition and healthiness e.g. high protein (~ 20%) and low fat content (< 2.2%) and a favourable polyunsaturated to saturated fatty acids (FA) ratio (PUFA:SFA) of < 0.45 for the *Longissimus lumborum* (LL) muscle, which is the ratio recommended as beneficial for the human diet. The dominant FA were palmitic (C16:0), stearic (C18:0) (saturated fatty acids), linoleic (C18:2ω6) (polyunsaturated fatty acids), oleic (C18:1ω9c) (monounsaturated fatty acids) (Chapter 6). It was therefore not considered necessary to market the meat according to sex but there was still some research required to determine whether age could significantly influence physical and chemical composition, and ultimately consumer desirability and acceptance (Chapter 7). There have been reports that the fresh meat from warthogs sometimes exhibits a flavour that is compared to boar taint, which is an undesirable odour and flavour that may occur in the meat from entire male domestic pigs (*Sus scrofa*), but has been associated with warthog meat from both genders and animals of different age classes. Although no research has been conducted of this particular aroma or flavour in the meat from warthogs or other wild suid species, it is commonly believed to pertain only to adult males.

In order to elucidate on the undesirable flavours and overall sensory profile of warthog meat, the sensory profile of warthog meat (*Longissimus lumborum*) was determined as influenced by sex and age (Chapter 7). The yields and physical characteristics appeared to be similar in general to those found in Chapter 6. Overall, age appeared to have a greater influence compared to gender on the sensory attributes. An undesirable odour and flavour detected were described as "sour/sweaty" and "fishy" and not as "boar taint", and were scored higher in juveniles than adults, but not between sexes within age class. The most surprising results were that the undesirable aroma and flavour described here as "sour/sweaty" was found not only in adult males as opposed to popular belief, but also in the juveniles. The textural (mouth-feel) attributes also differed among the four groups, with the meat from adult warthogs considered less tender and with more residue. However, the overall tenderness of warthog meat was high. It was proposed that total moisture content is an important factor influencing the sensory profile and mouth-feel experience of warthog meat considering the overall low total fat. In additional, the sensory profile of the meat was dominated by pork aroma and flavour and not described as being gamey. This raises the question of whether gamey attributes should be described as 'associated with game meat', and its aptness to distinguish among meat from different species as suggested by Rødbotten et al. (2004, Chapter 7). Again, the influence of sex and age on physical characteristics and healthiness of cooked warthog meat were considered negligible, which was high in protein (~32%) and low in total fat (< 2%). The dominant FA were palmitic, stearic, linoleic and arachidonic (C20:4ω6), while only palmitoleic (C16:1), arachidonic acids and the omega 6:omega 3 (ω6:ω3) FA ratio differed among the four groups. However, the PUFA:SFA ratio of the LL muscle from all four groups was > 0.45, and the ω6:ω3 ratio < 4, which are the ratios recommended for the human diet (Warris, 2000). In this study arachidonic acid was found at higher levels in the LL muscle from adult warthogs compared to Chapter 6 (1.18 and 0.36mg·g^{-1}, respectively), while oleic acid was found at low levels in the LL muscle from adult warthogs compared to Chapter 6 (0.01 and 2.25mg·g^{-1}, respectively). These differences were attributed to the differences in the regional and seasonal diet of warthogs, as the warthogs from Chapter 6 were culled on agricultural lands, while the warthogs from Chapter 7 were culled on a game reserve. The study (Chapter 7) suggested that the sensory profile of warthog meat requires further investigation as the occurrence of undesirable flavours could affect consumer desirability and acceptance. In addition, from the findings in Chapter 6 and 8, future studies should also aim to determine the effect of extrinsic factors on meat quality such as diet, season, production region, considering the wide-spread distribution of warthogs in South Africa and their free-roaming nature.

As increased production and utilization of warthog meat has been proposed as a strategy to encourage warthog management, the use of meat in processed products could extend the value chain of game meat production especially as forequarter muscles for example are considered less desired for whole meat cut consumption. In Chapter 8 a processed product of warthog meat in the form of back bacon (*Longissimus thoracis et lumborum* [LTL]) was produced with the meat derived from adult and juvenile boars and sows, considering the effect of sex and age on sensory characteristics. The back bacon was described as having a profile of typical bacon and smoky aroma and flavour, and salty flavour, as well as being tender and juicy (Chapter 8). There were no differences pertaining to sex and age in bacon's chemical composition, which was high in protein (~29%) and low in total fat (< 2%) content, while palmitic, stearic, linoleic, oleic and arachidonic were the dominant fatty acids (FA). This was expected to a certain degree as the *Longissimus lumborum* (LL) muscles used for back bacon production were sourced from the same warthogs culled in Chapter 7. However, the FA composition of the cooked LL and back bacon may have been influenced by the storage (freezing), processing (pertaining to bacon production) and cooking, with the back bacon having an increased proportion of monounsaturated (MUFA) and a decreased proportion of saturated (SFA) and polyunsaturated (PUFA) FA compared to the cooked LL muscle in Chapter 7. The higher MUFA content is attributed to the higher content of oleic acid (C18:1n9t) in the back bacon. However, the PUFA:SFA and ω6:ω3 ratio of the back bacon was not different to that of cooked warthog LL (Chapter 7). The results from this study indicated that warthog meat can be converted to healthy processed products without compromising the sensory attributes associated with the product, and provides further evidence that processes such as curing and smoking are able to reduce or 'mask' undesirable flavours. The addition of nitrite and contribution of smoking compounds are suggested as being responsible for this conversion, and the development of specific aromatic compounds associated with bacon. The parameters of sex and gender did not influence the sensory profile of warthog back bacon.

Game meat is known to have a low total fat content and is therefore considered more healthy compared to the meat from domestic animals, but reducing the fat content of processed meat products should not adversely affect eating quality and consumers' expectations. With these considerations in mind, a ready-to-eat processed product was produced with warthog meat sourced from the warthogs culled in Chapter 5, which consisted of all the meat trimmed from carcasses after the six skeletal muscles were removed, with exception of the belly (Chapter 9). The study compared the chemical and sensory characteristics and consumer preference of cabanossi produced with warthog meat and with domestic pork. The warthog and pork cabanossi had similar total moisture (59.0% and 54.3%, respectively) and protein (26.3% and 24.2%, respectively) contents, while the warthog cabanossi was lower in total fat content (6.9% and 13.7%, respectively) (Swanepoel, Leslie, & Hoffman, 2016, Chapter 9). There were no differences in consumer preference of the appearance and taste between the two types of cabanossi.

In addition, the majority of the consumers (91%) supported the use of game meat in meat products. The study concluded that warthog meat can be processed without compromising the technical or organoleptic properties associated with the product, similar to the results of Chapter 8 for warthog back bacon. It is therefore considered possible to produce nutritious low-fat meat products by using the trimmed meat from game animal carcasses, which could contribute to the niche game meat market in South Africa.

Despite the encouraging results found in this study regarding the quality and properties of warthog meat for game meat consumption, there are still many research questions regarding the distribution, impacts, utilization and management of warthog populations in South Africa, as this study is one of the first and most recent to address an introduced population in South Africa in term of these aspects. The study highlighted a number of important avenues identified for further research including the potential and actual (quantifiable) adverse impacts associated with expanding warthog populations. An extensive literature review (Chapter 2) attempted to review all of the available research on the impacts of warthogs on the known and potential impacts of warthogs on the natural and agricultural environment in their natural and introduced distribution, however there is limited research available focussing on South Africa. Since agricultural producers regard warthogs as a high risk species (Nyafu, 2009, Swanepoel et al., 2016) it is necessary to determine the extent of their impacts as Chapter 10 contended the species might be classified as a damage causing species, opposed to an alien or invasive species under new legislation. This includes increased research efforts on their potential to introduce and transmit animal and zoonotic diseases, considering the possibility that producing warthog meat from certified disease-free areas might encourage warthog meat consumption and possibly allow for meat/meat product exports in the future.

Furthermore, the influence of other extrinsic factors on the quality and production of warthog meat needs to be investigated pertaining to production parameters and consumer acceptability. However the use of warthog meat in processed meat products appears to reduce the effect of intrinsic factors on the organoleptic properties of the meat. This is an important avenue for further research as it could increase game meat consumption and broaden the scope of game meat utilization in South Africa, and potentially globally. As mentioned in Chapter 10, the consumption of game meat is an important factor that promotes the social acceptability of hunting, which is integral to wildlife management and utilization strategies. The study in its entirety provides baseline information pertaining to and influencing warthog yields and meat quality characteristics, and concludes that warthogs can be utilized as a game animal for meat production and utilization, with the benefit of producing an overall lean meat with desirable properties for processing. Encouraging warthog meat utilization and consumption could aid in the management of introduced warthogs and mitigation of the damages experienced by agricultural producers.

In Chapter 10, the management of introduced warthogs in terms of hunting is discussed, as well as the possibilities for utilizing warthogs as a game animal including alternative uses that assign a monetary and aesthetic value to warthogs, as mentioned in Swanepoel et al. (2016, Chapter 4). In addition, it was noted that their interaction with the environment in terms of life history traits has not been investigated in areas of introduction. The vital characteristics of population dynamics are used to develop and determine the sensitivity of a population to management strategies, and ultimately test the effectiveness of applied management. Researching this would appear to be the next logical step towards advancing wildlife management science and the knowledge of introduced and free-roaming species.

References

Bekker, J. L., Hoffman, L. C., & Jooste, P. J. (2012). Wildlife-associated zoonotic diseases in some southern African countries in relation to game meat safety: A review. *The Onderstepoort Journal of Veterinary Research*, *79*, E1–E12. doi:10.4102/ojvr.v79i1.422

Department of Environmental Affairs (DEA). (2010). National Environmental Management: Biodiversity Act 2004 (Act No. 10 of 2004). Draft norms and standards for management of damage-causing animals in South Africa. Government Gazette (33806). Retrieved from https://www.environment.gov.za/sites/default/files/gazetted_notices/nemba_draftnormsandstandards_g33806gen1084.pdf

Department of Environmental Affairs (DEA). (2014). National Environmental Management: Biodiversity Act 2004 (Act No. 10 of 2004): Alien and Invasive Species Regulations. Government Gazette (36683). doi:http://dx.doi.org/9771682584003-32963

Department of Environmental Affairs (DEA). (2015). National Environmental Management: Biodiversity Act, 2004 (Act No. 10 of 2004). *Norms and standards for the translocation of indigenous species in South Africa. Volume 595, Government Gazette (38395).* Pages 1–16. Government Printer: Pretoria, South Africa. Retrieved from www.gpwinline.co.za. doi:http://dx.doi.org/9771682584003-32963. Accessed 15 May 2014.

Erasmus, S. W., Muller, M., Van der Rijst, M., & Hoffman, L. C. (2016). Stable isotope ratio analysis: A potential analytical tool for the authentication of South African lamb meat. *Food Chemistry*, *192*, 997–1005. doi:10.1016/j.foodchem.2015.07.121

Hoffman, L. C., Mostert, A. C., & Laubscher, L. L. (2009). Meat quality of kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*): The effect of gender and age on the fatty acid profile, cholesterol content and sensory characteristics of kudu and impala meat. *Meat Science*, *83*, 737–743. doi:10.1016/j.meatsci.2009.08.026

Matthee, S., Swanepoel, M., Van der Mescht, L., Leslie, A. J. & Hoffman, L. C. (2013). Ectoparasites of a non-indigenous warthog population, *Phacochoerus africanus*, in the Free State Province, South Africa. *African Zoology, 48*, 259-265.

Neethling, J., Britz, T. J., & Hoffman, L. C. (2014). Impact of season on the fatty acid profiles of male and female blesbok (*Damaliscus pygargus phillipsi*) muscles. *Meat Science*, *98*, 599–606. doi:10.1016/j.meatsci.2014.06.030

Neethling, J., Hoffman, L. C., & Britz, T. J. (2013). Impact of season on the chemical composition of male and female blesbok (*Damaliscus pygargus phillipsi*) muscles. *Journal of the Science of Food and Agriculture*, *94*, 424–431. doi:10.1002/jsfa.6281

Nyafu, K. (2009). *Warthog as an introduced species in the Eastern Cape*. MSc thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

Rødbotten, M., Kubberød, E., Lea, P., & Ueland, Ø. (2004). A sensory map of the meat universe: Sensory profile of meat from 15 species. *Meat Science*, *68*, 137–44. doi:10.1016/j.meatsci.2004.02.016

Swanepoel, M., Leslie, A. J. & Hoffman, L. C. (2014). Carcass yield of common warthog (*Phacochoerus africanus*); influence of season and sex. *South African Journal of Wildlife Research, 44,* 179-188.

Swanepoel, M., Leslie, A. J., & Hoffman, L. C. (2016). Farmers' perceptions of the extra-limital common warthog in the Northern Cape and Free State provinces, South Africa. *Wildlife Society Bulletin*. doi:10.1002/wsb.617.

Swanepoel, M., Leslie, A. J. & Hoffman, L. C. (2016). Comparative analyses of the chemical and sensory parameters and consumer preference of a semi-dried smoked meat product (cabanossi) produced with warthog (*Phacochoerus africanus*) and domestic pork meat. *Meat Science, 114*, 103–113. doi:10.1016/j.meatsci.2015.12.002.

Swanepoel, M., Schulze, E., & Cumming, D. (in press.). A conservation assessment of *Phacochoerus africanus*. In: M. F. Child, D. Raimondo, E. Do Linh San, L. Roxburgh & H. Davies-Mostert (Eds.), *The Red List of Mammals of South Africa, Swaziland and Lesotho*. Pretoria, South Africa: South African National Biodiversity Institute and Endangered Wildlife Trust.

Valencak, T. G., Gamsjäger, L., Ohrnberger, S., Culbert, N. J., & Ruf, T. (2015). Healthy n-6/n-3 fatty acid composition from five European game meat species remains after cooking. *BMC Research Notes*, *8*, 273. doi:10.1186/s13104-015-1254-1

Warris, P. (2000). *Meat Science*. Oxon: CAB Publishing.

Addendum A

Ectoparasites of a non-indigenous warthog population, *Phacochoerus africanus*, in the Free State Province, South Africa*

Abstract

A population of the common warthog, *Phacochoerus africanus*, recently became established on several farms in the Free State Province, South Africa. The aim of the study was to record ectoparasite species that occur on this non-indigenous population and to compare the parasite abundance and prevalence at three different times during 2011. Forty six warthogs were culled in autumn (15), winter (16) and spring (15). Each individual warthog was screened for ectoparasites for 7-10 minutes by 3-4 persons. Parasites were removed using forceps and stored in 70% ethanol. Ticks were identified by an expert taxonomist, while fleas and lice were identified using published books containing their respective taxonomic keys. A single flea (*Echidnophaga larina*) and louse (*Haematopinus phacocheri*) species and three tick species (*Hyalomma truncatum*, *Rhipicephalus gertrudae* and *Rhipicephalus simus*) were recovered from 46 warthogs. The louse and flea were the most abundant ectoparasite taxa, while the ticks had lower mean abundances. This is the first record of the tick *R. gertrudae* on warthogs in South Africa to date. Temporal variation in parasite abundance was observed. The louse was most abundant during spring and summer, while the flea preferred cooler and drier winter conditions. *Hyalomma truncatum* and *R. gertrudae* both preferred warmer spring conditions. In general, parasite species richness in the non-indigenous host population was low, which could support the parasite release hypothesis.

Keywords: ectoparasites, warthog, *Phacochoerus africanus*

*Matthee, S., Swanepoel, M., Van der Mescht, L., Leslie, A. J. & Hoffman, L. C. (2013). Ectoparasites of a non-indigenous warthog population, *Phacochoerus africanus*, in the Free State Province, South Africa. *African Zoology, 48*, 259-265.

1 Introduction

The common warthog, *Phacochoerus africanus*, is endemic to the northern, north-eastern and eastern parts of South Africa, though isolated pockets do occur in the Eastern Cape Province through their introduction to reserves (Skinner & Chimimba, 2005). They also occur naturally in the neighbouring countries to the north and west of South Africa (Skinner & Chimimba, 2005). Historical records indicate that an extinct species, the Cape warthog (*Phacochoerus aethiopicus*), occurred naturally in the southern region of South Africa, including the Free State Province (D'Huart & Grubb 2001, Skead, 2007).

Phacochoerus africanus can harbour several ecto- and endoparasite taxa, with macroparasite diversity spanning a range of helminths (Round 1968), fly larvae (Zumpt, 1965), fleas (Segerman, 1995), lice (Ledge,r 1980) and ticks (Theiler, 1962). To date, few quantitative studies have been conducted on the parasites that are associated with this host species in South Africa. Horak et al., (1983) examined 38 individuals in Namibia and Horak et al., (1988) and Boomker et al., (1991) studied 69 and 41 individuals in Mpumalanga, respectively. It is evident from these studies that the parasite assemblages on warthogs in the native northern parts of South Africa are quite diverse and include several species of ticks, fleas, helminths and one louse (Horak et al., 1983, Horak et al., 1988, Boomker et al., 1991). In particular they noted the presence of argasid ticks on warthogs in the northern regions of South Africa and Namibia. One of the tick species, *Ornithodoros moubata* complex, plays an important role in the epidemiology of African swine fever in South Africa and the rest of the African continent (Penrith, 2009).

Populations of common warthog were recently established at several locations in the Free State Province through multiple introductions onto farms and reserves from 1980 onwards. The aim of this study was to record the ectoparasite diversity of a non-indigenous warthog population in the Free State Province (FSP). It was predicted that the parasite species richness in the new population would be lower given the fact that *P. africanus* is not endemic to the region. A common phenomenon in invasion ecology is the "enemy (parasite) release hypothesis" (Drake, 2003, Torchin et al., 2003, Britton, 2013). In theory, non-indigenous species leave their natural parasites behind in their native range and would thus have lower parasite species richness in introduced areas (Torchin et al., 2003). Parasite abundance varies seasonally. In concurrence, vegetation type and rainfall regimes can also affect temporal variation in mean abundances. The second aim of this study was thus to compare the parasite abundance and prevalence on this host during three different sampling periods (autumn, winter and spring).

2 Research methods and design

2.1 Study materials, setting and design

Warthogs were culled on six farms, practising various forms of agriculture, in the Boshoff district, 120 km southeast of Bloemfontein, FSP, South Africa (28° 33' 0" N, 25° 15' 0" E) during 2011. Culling was done over seven days during three different sampling periods (March = autumn, June = winter and October = spring). A total of 46 animals (15, 16 and 15, respectively) of which 36 individuals were adult and the rest (10 individuals) were juveniles. The sex ratio was approximately 1:1 (24 females and 22 male). The mass of the animals ranged from 14.30-91.56 kg (mean = 52.69 kg).

2.2 Parasite recovery and identification

Each individual warthog was examined immediately after the animal was culled, and then processed in the field. Only qualitative sampling of the body was possible. Each animal was screened for 7-10 minutes by 3-4 people. Mane hairs were collected, in most cases, and placed in plastic bags. Ticks, fleas, and lice were removed from the body using forceps and separately placed in sample bottles filled with 70% ethanol. All samples were brought to Stellenbosch University for identification. Fleas and lice were identified using taxonomic keys (books) (Ledger, 1980, Segerman, 1995) and ticks were identified by a tick taxonomist (I. G. Horak).

2.3 Ethical considerations

This project was approved by the Animal Use and Care Committee at Stellenbosch University, under project number 11LV_HOF02.

3 Results

3.1 Parasite abundance and prevalence

Five different ectoparasite species were recorded (Table 1), including a flea species (*Echidnophaga larina*), a louse species (*Haematopinus phacochoeri*) and three tick species (*Hyalomma truncatum*, *Rhipicephalus gertrudae* and *R. simus*). The louse was the most abundant species (6.11 ± 1.78), followed by the flea (2.30 ± 0.67). The parasite sex ratio was biased towards females for both the louse (1:3.5) and flea (1:5.6). Tick abundance was generally lower compared to lice and fleas. Parasite prevalence followed a similar pattern with 39-45% of the warthog harbouring fleas and lice compared to 4-26% for the three tick species (Table 1). Male warthogs were parasitized by the five different ectoparasite species recorded, while only four of the recorded species were found on female animals

(*R. simus* was absent on females). Male individuals generally also seem to be infested by a higher abundance of ectoparasites than females (Table 1).

Table 1. Parasite infestation parameters of ectoparasites recorded from 46 warthogs in the Free State Province, South Africa.

Host sex	n		*E. larina*	*H. phacochoeri*	*H. truncatum*	*R. simus*	*R. gertrudae*	Total count
Both	46	Prevalence (%)	39.13	45.65	26.09	4.35	10.87	
		Sum	106	281	28	2	36	453
		Mean (± SE)	2.30 ± 0.67	6.11 ± 1.78	0.61 ± 0.20	0.04 ± 0.03	0.78 ± 0.53	
Female	24	Prevalence (%)	41.67	45.83	37.50	0	8.33	
		Sum	55	128	25	0	12	220
		Mean (± SE)	2.29 ± 0.81	5.33 ± 2.15	1.04 ± 0.35	0	0.5 ± 0.46	
Male	22	Prevalence (%)	36.36	45.45	13.64	9.09	13.64	
		Sum	51	153	3	2	24	233
		Mean (± SE)	2.32 ± 2.70	6.95 ± 5.54	0.14 ± 1.73	0.09 ± 0.05	1.09 ± 0.99	

3.2 Temporal variation

Mean abundances for the individual parasite species varied temporally, though no consistent pattern was evident. *Echidnophaga larina* was present in higher numbers in March (autumn) and October (spring), while *H. phacochoeri* was more abundant during March and June (Figure1). No ticks were recorded on the warthogs in June (mid-winter). *Hyalomma truncatum* was more abundant in March and October and *R. gertrudae* peaked in October. *Rhipicephalus simus* was only recorded on the warthogs during the March sampling period (Figure 2).

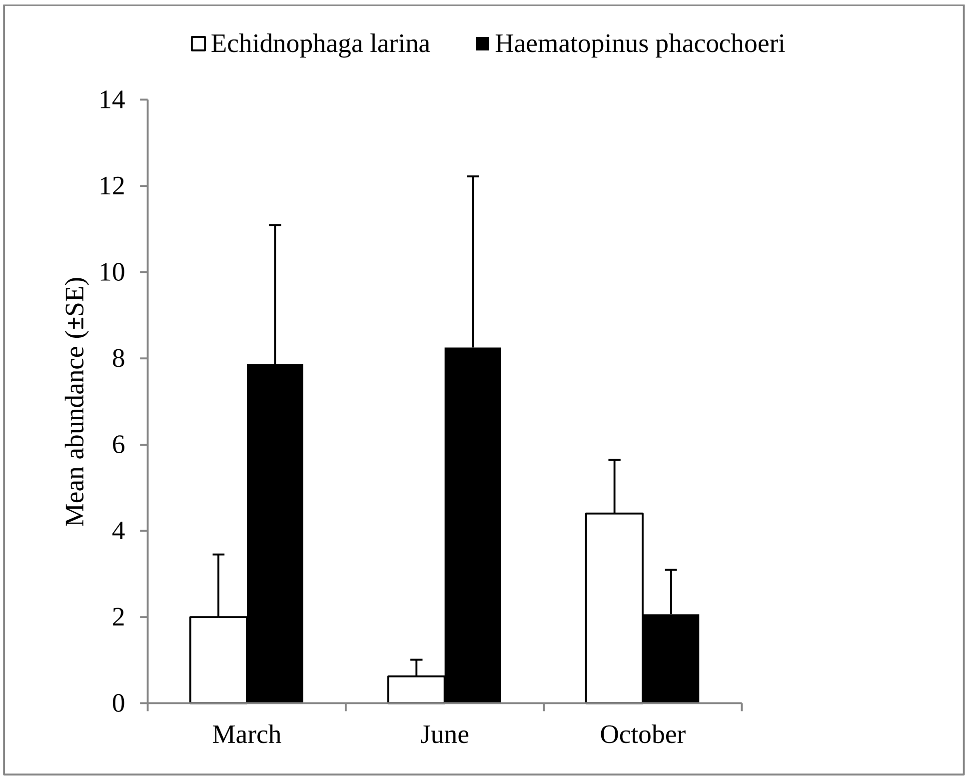

Figure 1. Seasonal abundance of *Echidnophaga larina* and *Haematopinus phacochoeri* on warthogs in the Free State Province.

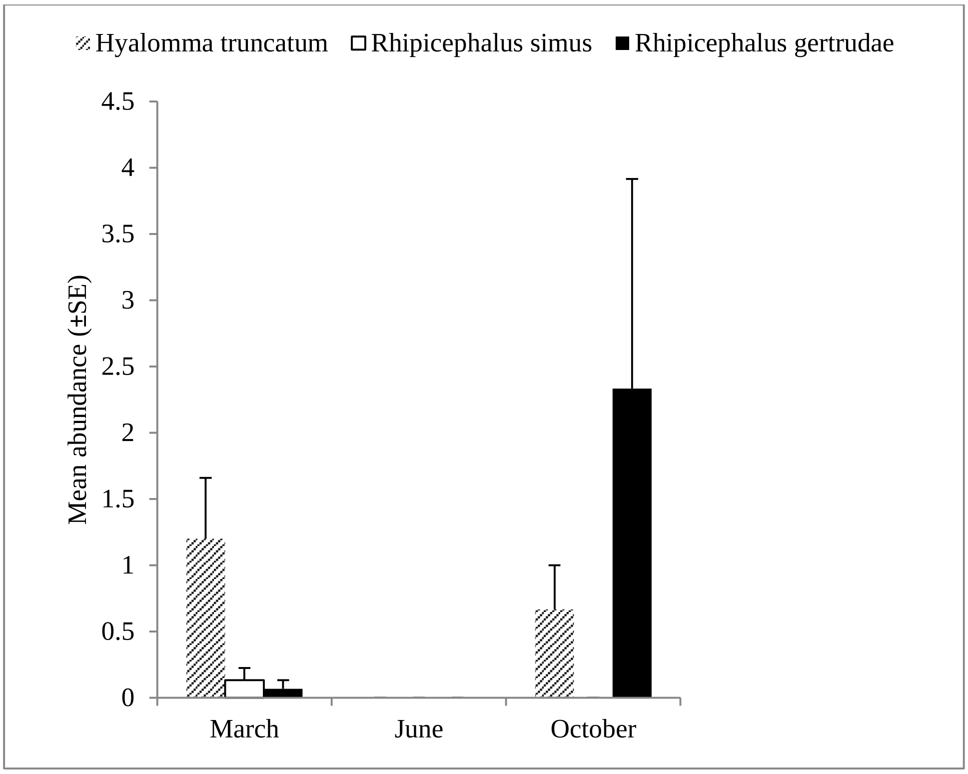

Figure 2. Seasonal abundance of *Hyalomma truncatum*, *Rhipicephalus gertrudae* and *Rhipicephalus simus* on warthogs in the Free State Province.

4 Discussion

Most of the parasite species recorded from warthogs in the present study were previously recorded on this host (Table 2, Horak et al., 1983, Horak et al., 1988, Boomker et al., 1991). *Rhipicephalus gertrudae* was the only ectoparasite species which has not been previously recorded on this host. However, the total parasite abundance was lower in the present study when compared to previous studies (Horak et al., 1983, Horak et al., 1988, Boomker et al., 1991). A possible reason for this may be the difference in the parasite recovery techniques that were used, the present study using visual examination, while a more quantitative brush technique was used in the others.

A louse, *H. phacochoeri,* and flea, *E. larina*, were the two most abundant parasite species in the present study. Similar results were found in Mpumalanga (Horak et al., 1988, Boomker et al., 1991) and Namibia (Horak et al., 1983). The large sucking louse, *H. phacochoeri*, seems to prefer warthogs (Ledger, 1980). The high abundance and prevalence of the louse in the FSP was also evident in two studies conducted in Mpumalanga and one in Namibia (Horak et al., 1983, Horak et al., 1988, Boomker et al., 1991). *Echidnophaga larina* is a stick-tight flea and was the second most abundant ectoparasite in the present study. Two previous studies in Mpumalanga (Horak et al., 1988, Boomker et al., 1991) recorded two species of *Echidnophaga* on warthog, *E. larina* and *E. inexpectata*. Beaucourno and Horak

(1994) have since placed the latter species in a new genus: *Phacopsylla*. The studies conducted in the northern parts of South Africa also recorded a second flea, *Moeopsylla sjoestedti*, however, this flea, together with *P. inexpectata*, seems to be restricted to the north-eastern parts of South Africa and Zimbabwe (Segerman, 1995). Tick species richness in the present study was lower (three species) compared to the species richness recorded from warthogs in the northern savannah regions of South Africa (8 and 9 species) and Namibia (7 species, Table 2). Lower tick species richness in the non-indigenous FSP population may be due to geographic variation in tick species distribution across southern Africa, resulting in the absence of certain tick species in the FSP (most of the abundant tick species on warthogs occur in the northern regions of the country) (Howell et al., 1978, Walker 1991, Walker et al., 2000). Alternatively, the lower species richness evident in the present study may support the hypothesis that depauperate parasite communities are often associated with host populations that establish in non-native habitats (Dobson & May, 1986, Torchin et al., 2003, Kvach & Stepien, 2008, Halbritter et al., 2011). In addition to a loss of species, introduced populations may gain additional parasite species that are endemic in the specific area or region (Smith et al., 2004). Generalist parasite species (i.e. have a broad host preference) should have a higher probability of infesting introduced host species compared to host-specific species (Ricklefs et al., 2004). The presence of *R. gertrudae* on warthog in the FSP supports this suggestion. *Rhipicephalus getrudae* predominantly occurs in the southern and south central parts of South Africa, which includes the grassland vegetation of the FSP (Walker et al., 2000). The immature stages of this tick prefer smaller mammals such as rodents (Walker, 1991, Walker et al., 2000, Matthee et al., 2007) while the adult stages occur on a wide range of wildlife species such as antelope, carnivores and rodents (Walker 1991, Walker et al., 2000).

Table 2. Check-list of flea, lice and tick species recorded from warthogs at various localities in South and southern Africa.

Arthropod species	Localities			
	Present study	Kruger National Park[1]	Hoedspruit[2]	Namibia[3]
Fleas				
Echidnophaga larina	X	X	X	X
Echidnophaga inexpectata	-	X	X	-
Moeopsylla sjoestedti	-	X	X	-
Lice				
Haematopinus phacochoeri	X	X	X	X
Ixodid ticks				
Amblyomma hebraeum	-	X	X	-
Amblyomma marmoreum	-	-	X	-
Boophilus decoloratus	-	X	X	-
Hyalomma marginatum rufipes	-	-	-	X
Hyalomma truncatum	X	X	X	X
Rhipicephalus appendiculatus	-	X	X	-
Rhipicephaluus evertsi evertsi	-	X	X	-
Rhipicephaluus evertsi mimeticus	-	-	-	X
Rhipicephalus gertrudae	X	-	-	-
Rhipicephalus longiceps	-	-	-	X
Rhipicephalus oculatus	-	-	-	X
Rhipicephalus simus	X	X	X	X
Rhipicephalus zambeziensis	-	X	X	-
Argasid ticks				
Ornithodoros porcinus porcinus	-	X	X	-
Ornithodoros moubata	-	-	-	X

[1]Horak et al., 1988.
[2]Boomker et al., 1991.
[3]Horak et al., 1983.

From this study it appears that male warthog harboured more tick species and also had a higher abundance of ectoparasites when compared to female warthog. Unfortunately, none of the previous studies provided data on host sex differences, though Horak et al., (1988) did note an age effect, with animals progressively attaining more parasite species with age. Gender-bias' in parasite infestation appears to be commonly associated with vertebrate hosts, with male-biased infestation frequently observed in mammals (Moore & Wilson 2002). There are several reasons for this pattern, which include the immune-suppressive effect of testosterone, higher mobility, less frequent grooming and larger body size in male hosts compared to females (Mooring & Hart, 1995, Moore & Wilson, 2002, Bandilla et al., 2005, Cox & Henry, 2007, Hillegass et al., 2008).

Temporal variation in mean abundance was noted for the parasite taxa in the present study, *E. larina* was present in higher numbers in autumn (March) and spring (October). This pattern is consistent with two studies conducted in Mpumalanga where peak abundances were recorded on the warthogs in early winter (May-July) and spring/early summer (September-November) (Horak et al., 1988, Boomker et al., 1991). In contrast, it seems that *H. phacochoeri* prefers cooler winter months (March and June) in the FSP and also in Mpumalanga and Namibia (Horak et al., 1983, Horak et al., 1988, Boomker et al., 1991). Similar to previous studies, the FSP falls within the summer rainfall region. This might explain the overlap in activity periods for fleas and lice, across regions. *Hyalomma truncatum* was most abundant on the warthogs in March and October in the present study. It is possible that the adult stages of this tick are abundant during the warmer spring and summer months. Unfortunately no clear temporal pattern was observed for this tick in any of the previous studies on warthogs. However, increased abundance during spring to summer was recorded previously on cattle in the FSP (Fourie & Horak, 1990), sheep in the Western Cape Province (Horak & Fourie, 1992) and on cattle and large antelope at various localities in South Africa (Horak et al., 2002). In the present study, very low abundances were recorded for *R. simus* and it was only recorded in autumn (March). This is in contrast to a spring-summer peak that was recorded on warthog in Mpumalanga (Horak et al., 1988, Boomker et al., 1991). The low abundance might be due to the fact that the grassland region of the FSP largely falls outside of its preferred distribution range. The warthog population in the FSP most probably originated from localities in the north and thus the parasites could have been brought in with the host. At present it is uncertain to say whether *R. simus* has adapted to the climatic conditions in the FSP. If the species does establish then there is a potential disease risk as *R. simus* has been shown to transmit *Babesia trautmanni* to domestic pigs (De Waal et al., 1992) and toxins to calves and lambs (Norval & Mason, 1981). In the present study, peak abundance was recorded for *R. gertrudae* on warthog in October. As mentioned before, this is the first record of this tick on warthog in South Africa, thus it is not possible to compare the seasonal pattern recorded in the present study with other studies. However, studies conducted on dogs in the Western Cape Province recorded increased abundances of adult ticks from August to October (Horak & Matthee, 2003).

The present study provides a checklist for ectoparasite species associated with a warthog population established in a non-native region. It is evident that parasite related factors, such as climatic preference, level of host association and specificity play an important role in shaping the observed patterns.

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7 References

Bandilla, M., Hakalathi, T., Hudson, P. J. & Valtonen, E.T. (2005). Aggregation of *Argulus coregoni* (Crustacea: Branchiura) on rainbow trout (*Oncorhynchus mykiss*): A consequence of host susceptibility or exposure? *Parasitology, 130*, 169–176.

Beaucourno, J-C. & Horak, I. G. (1994). *Phacopsylla* gen. nov. for *Echidnophaga inexpectata* Smit, 1950 (Siphonaptera, Pulicidae). *African Zoology, 108*, 133-140.

Boomker, J., Horak, I. G., Booyse, D. G. & Meyer, S. (1991). Parasites of South African wildlife. VIII. Helminth and arthropod parasites of warthogs, *Phacochoerus aethiopicus*, in the eastern Transvaal. *Onderstepoort Journal of Veterinary Research, 58*, 195-202.

Britton, J. R. (2013). Introduced parasites in food webs: new species, shifting structures? *Trends in Ecology and Evolution, 28*, 93–99.

Cox, R. M. & Henry, J-A. (2007). Increased mite parasitism as a cost of testosterone in male striped plateau lizards *Sceloporus virgatus*. *Functional Ecology ,21*, 327–334.

De Waal, D. T., Lopez Rebollar, L. M. & Potgieter, F. T. (1992). The transovarial transmission of *Babesia trautmanni* by *Rhipicephalus simus* to domestic pigs. *Onderstepoort Journal of Veterinary Research, 59*, 219-21.

D'Huart, J. & Grubb, P. (2001). Distribution of the common warthog (*Phacochoerus africanus*) and the desert warthog (*Phacochoerus aethiopicus*) in the Horn of Africa. *African Journal of Ecology, 39*, 156-169.

Dobson, A. P. & May, R. M. (1986). Patterns of invasions by pathogens and parasites. In H.A. Mooney & J.A. Drake (Eds.). *Ecology of Biological Invasions of North America and Hawaii* (pp 58–76). New York: Springer.

Drake, J. M. (2003). The paradox of the parasites: implications for biological invasion. *Proceedings of the Royal Society of London B, 270*, S133-S135.

Fourie, L. J. & Horak, I. G. (1990). Parasites of cattle in the south-western Orange Free State. *Journal of the South African Veterinary Association, 61*, 27-28.

Halbritter, A. H., Carroll, G. C., Güsewell, S. & Roy, B. A. (2011). Testing assumptions of the enemy release hypothesis: generalist versus specialist enemies of the grass *Brachypodium sylvaticum*. *Mycologia, 104*, 34-44.

Hillegass, M. A., Waterman, J. M. & Roth, J. D. (2008). The influence of sex and sociality on parasite loads in an African ground squirrel. *Behavioral Ecology, 19*, 1006–1011.

Horak, I. G., Boomker, J., De Vos, V. & Potgieter, F. T. (1988). Parasites of domestic and wild animals in South Africa. XXIII. Helminth and arthropod parasites of warthogs, *Phacochoerus aethiopicus*, in the eastern Transvaal Lowveld. *Onderstepoort Journal of Veterinary Research, 55*, 145-152.

Horak, I. G., Biggs, H. C., Hanssen, T. S. & Hanssen, R. E. (1983). The prevalence of helminth and arthropod parasites of warthog, *Phacochoerus aethiopicus*, in South West Africa/Namibia. *Onderstepoort Journal of Veterinary Research,* 50, 145-148.

Horak, I. G. & Fourie, L. J. (1992). Parasites of domestic and wild animals in South Africa. XXXI. Adult ixodid ticks on sheep in the Cape Province and in the Orange Free State. *Onderstepoort Journal of Veterinary Research,* 59, 275-283.

Horak, I. G., Fourie, L. J., Heyne, H., Walker, J. B. & Needam, G. R. (2002). Ixodid ticks feeding on humans in South Africa: with notes on preferred hosts, geographic distribution, seasonal occurrence and transmission of pathogens. *Experimental and Applied Acarology, 27*, 113-136.

Horak, I. G. & Matthee, S. (2003). Parasites of domestic and wild animals in South Africa. XLIII. Ixodid ticks of domestic dogs and cats in the Western Cape Province. *Onderstepoort Journal of Veterinary Research, 70* , 187-195.

Howell, C. J., Walker, J. B. And Neville, E. M. (1978). *Ticks, Mites and Insects Infesting Domestic Animals in South Africa. Part 1. Description and Biology*. Science Bulletin No. 393. Department of Agricultural Technical Services, Pretoria.

Kvach, Y. & Stepien, C.A. (2008). Metazoan parasites of introduced round and tubenose gobies in the great lakes: support for the "enemy release hypothesis". *Journal of Great Lakes Research, 34*, 23-35.

Ledger, J. A. 1980. *The arthropod parasites of vertebrates in Africa south of the Sahara. Volume IV. Phthiraptera (Insecta)*. Publications of the South African Institute for Medical Research No. 56 (pp 327). Johannesburg, South Africa: South African Institute for Medical Research.

Matthee, S., Horak, I. G., Beaucournu, J-C., Durden, L. A., Ueckermann, E. A. & Mcgeoch, M. A. (2007). Epifaunistic Arthropod Parasites of the Four-Striped Mouse, *Rhabdomys pumilio*, in the Western Cape Province, South Africa. *Journal of Parasitology, 93*, 47-59.

Matthee, S., Mcgeoch, M. A. & Krasnov, B. R. (2010). Parasite-specific variation and the extent of male-biased parasitism, an example with a South African rodent and ectoparasitic arthropods. *Parasitolog,y 137*, 651–660.

Moore, S. L. & Wilson, K. (2002). Parasites as a viability cost of sexual selection in natural populations of mammals. *Science, 297*, 2015–2018.

Mooring, M. S. & Hart, B. L. (1995). Differential grooming rate and tick load of territorial-male and female impala, *Aepyceros melampus*. *Behavioural Ecology, 6*, 94–101.

Norval, R. A. I. & Mason, C. A. (1981). The ticks of Zimbabwe II. The life cycle, distribution and hosts of *Rhipicephalus simus* (Koch, 1844). *Zimbabwe Veterinary Journal*, *12*, 2–9.

Penrith, M-L. (2009). African swine fever. Onderstepoort Journal of Veterinary Research, 76, 91–95.

Ricklefs, R. E., Fallon, S. M. & Bermingham, E. (2004). Evolutionary Relationships, Cospeciation, and Host Switching in Avian Malaria Parasites. *Systematic Biology, 53*, 111–119.

Round, M. C. (1968). Check list of the helminth parasites of African mammals of the Orders Carnivora, Tubulidentata, Proboscidea, Hyracoidea, Artiodactyla and Perissodactyla. *Technical Communication of the Commonwealth Bureau of Helmintholog,y 38*, 252.

Segerman, J. (1995). Siphonaptera of southern Africa. Handbook for the identification of fleas. Publications of the South African Institute for Medical Research. No. 57 (pp 264). Johannesburg, South Africa: South African Institute for Medical Research.

Skead, C. J., Boshoff, A. F., Kerley, G. I. H., & Lloyd, P. H. (2007). Historical incidence of the larger land mammals in the broader Eastern Cape (2nd ed) (pp 570). Port Elizabeth, South Africa: Port Elizabeth, Centre for African Conservation Ecology, Nelson Mandela Metropolitan University.

Skinner, J. D., & Chimimba, C. T. (2005). The mammals of the southern African subregion. Cambridge: Cambridge University Press.

Smith, S. A., Bell, G. & Bermingham, E. (2004). Cross-Cordillera exchange mediated by the Panama Canal increased the species richness of local freshwater fish assemblages. *Proceedings of the Royal Society of London B, 271*, 1889-1896.

Theiler, G. (1962). The Ixodoidea parasites of vertebrates in Africa south of the Sahara (Ethiopian Region). Project S. 9958. Report to the Director of Veterinary Services, Onderstepoort. Mimeographed.

Torchin, M. E., Lafferty, K. D., Dobson, A. P., Mckenzie, V. J. & Kuris, A. M. (2003). Introduced species and their missing parasites. *Nature, 421*, 628-630.

Walker, J. B. (1991). A review of the ixodid ticks (Acari, Ixodidae) occurring in southern Africa. *Onderstepoort Journal of Veterinary Research*, *58*, 81–105.

Walker, J. B., Keirans, J. E. & Horak, I. G. (2000). The genus *Rhipicephalus* (Acari, Ixodidae): A guide to the brown ticks of the world. Cambridge: Cambridge Academic Press.

Zumpt, F. (1965). Myiasis in man and animals in the Old World. London: Butterworths.