Ecology of plains zebra (*Equus quagga*) in Majete Wildlife Reserve, Malawi

by

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Declaration

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Abstract

Zebras occur throughout Africa and are responsible for sustaining the dynamics and overall well-being of the environments they reside in. However, zebras have experienced significant range reductions and restricted access to water and forage, as well as population declines within the last 100 years, contributing to the recent enlistment of plains zebra (*Equus quagga*) from Least Concern to Near Threatened on the IUCN Red List. In Majete Wildlife Reserve (MWR), located in southern Malawi, wildlife was almost completely extirpated from the reserve by 1985. In 2003 African Parks (Pty) Ltd. together with the Malawi's Department of National Parks and Wildlife (DNPW) aimed to restore the reserve to its former glory. Fences were constructed, law-enforcement was improved and wildlife was reintroduced, including 174 plains zebra (hereafter referred to as zebra). More than ten years after the species' initial reintroduction, zebra have successfully established within MWR. Prior to this study, no long-term monitoring was conducted on MWR's zebra post reintroduction. In this study, zebra demographics, diet, waterhole usage and behaviour was investigated.

The demography of zebra was determined with the use of an individual side-stripe database and an aerial survey. Of the estimated 571 zebra currently in the reserve, 243 were individually identified. Over the last few years, the population appears to have transitioned from the slower growth rate expected immediately after translocation to the rapid annual growth rate indicative of an approach toward carrying capacity. Adult zebra in the reserve currently exhibit a biased sex ratio of 1.0:0.8 (female:male). Population structure and organization is similar to established zebra populatons; however the formation of herds (multiple bands associating with each other) was never observed in MWR. In addition, stable isotope analysis was conducted to examine the seasonal diet of the species. Results confirmed that zebra are predominantly grazers that occasionally browse (trees, shrubs and forbs), even given the dominance of browse (dicotyledonous trees and shrubs) in the miombo woodland environment of Majete. The proportion of browse consumed, however, varied significantly among the seasons, with only 1.5% browse consumed during the late wet season compared to 10.2% in the late dry season.

Artificial waterhole usage by zebra was studied with the use of camera traps. Waterholes were predominantly visited at 09:00, 13:00 and 14:00. However, when natural surface water decreased and more animals aggregated around artificial waterholes, it appeared that zebra shifted their visitation time to avoid interspecific competition around these waterholes. Finally, the diurnal time budgets of this species indicated that family bands allocate 41.8% of their time to feeding behaviour, followed by resting (18.5%), locomotion (10.9%), vigilance (7.5%), maintenance (2.7%) and social behaviour (1.4%). In comparison, bachelor bands allocated 27.0% to vigilance behaviour, followed by locomotion (21.0%), feeding (18.4%), resting (15.4%), maintenance (6.4%) and social behaviour (2.4%). It is unknown if the relatively small amount of time spent feeding was compensated for nocturnally or is indicative of low graze availability during the dry season.

Based on the findings of this study, issues facing the conservation of zebra within MWR were identified and conservation and management options are presented.

Opsomming

Sebras kom regdeur Afrika voor en is verantwoordlik om die dinamika en welstand van die ekosisteem waarin hulle voorkom te onderhou. Binne die laaste 100 jaar, is hulle egter beïnvloed deur habitat verlies, beperkde toegang tot water en kos, sowel as ‘n afname in populasiegetalle. Hierdie het bygedra tot die onlangse verandering in die vlaktesebra (*Equus quagga*) se IUCN Rooi Lys klassifikasie vanaf Lae Risiko na Byna Bedreig. Die Majete Wildreservaat (MWR), wat in die suide van Malawi geleë is, was amper gestroop van alle wild teen 1985. In 2003 het African Parks (Pty) Ltd. saam met Malawi se Departement van Nationale Parke en Wild (DNPW) beoog om die reservaat te herleef. Heinings is opgerig, wetstoepassing is versterk en wild is gehervestig, insluitend 174 vlaktesebras (hierna slegs verwys as sebra). Nou, meer as tien jaar na die aanvanklike herlewing, is sebra suksesvol gevestig in die reservaat, maar geen lang-termyn navorsing is al gedoen op die reservaat se sebra na die herinstelling nie. In hierdie studie, is die demografie, dieet, watergatgebruik en gedrag van die sebra ondersoek.

Die demografie van die sebra is bepaal met behulp van ‘n individuele kant-streep databasis en ‘n lugopname. In totaal is 243 individue geidentifiseer van ‘n beraamde 571. Dit wil voorkom dat die populasie in die laaste paar jaar, vanaf ‘n stadiger bevolkingsgroeikoers, soos wat verwag word tydens die eerste paar jaar na hervestiging van wild, bevorder het na ‘n vinnige bevolkingsgroeikoers wat aandui dat die populasie die dra-kapasiteit benader. Volwasse sebra in die reservaat vertoon ‘n bevooroordeelde geslagsverhouding van 1.0:0.8 (vroulik:manlik). Daar is gevind dat die demografie soortgelyk is aan ander gevestigde populasies, alhoewel troppe (die samekoms van groepe) nooit waargeneem is in MWR nie. Verder is die dieet van sebra ondersoek deur gebruik te maak van stabiele isotoop analise van mismonsters. Resultate het bevestig dat sebra hoofsaaklik gras vreet en slegs af en toe blare sal eet, ongeag daarvan dat takvoer (tweesaadlobbige bome and bosse) meer algemeen bekombaar is in die miombo bos habitat van Majete. ‘n Duidelike seisoenale verskil in die persentasie blare wat gevreet is, is ook gevind. In die lae nat seisoen het hulle dieet slegs 1.5% takvoer bevat in vergelyking met 10.2% tydens die lae droë seisoen.

Die besoek aan kunsmatige watergate is ondersoek deur gebruik te maak van kamerastrikke. Kunsmatige watergate was hoofsaaklik besoek tydens 09:00, 13:00 en 14:00. Wanneer natuurlike waterbronne egter begin opdroog het en meer diere rondom die kunsmatige watergate begin saamdrom het, wil dit voorkom asof sebra hulle besoektye aan kunsmatige watergate verander het om interspesifieke kompetisie te vermy. Laastens, het die daglig tydsbegrotings van die spesie vasgestel dat familie groepe 41.8% van hulle tyd spandeer om te vreet, daarna om te rus (18.5%), te beweeg (10.9%), waaksaam te wees (7.5%), hulself te versorg (2.7%) en om sosiaal te verkeer (1.4%). Rondloper mannetjies spandeer weer die meerderheid van hulle tyd om waaksaam te wees (27.0%), gevolg deur te beweeg (21.0%), te vreet (18.4%), te rus (15.4%) en sosiaal te verkeer (2.4%). Dit is onbepaald of die relatiewe klein hoevelheid tyd wat deur die dag aan vreet spandeer was, gekompenseer word deur meer tydens die aand te vreet en of dit ‘n gevolg is van die skaarsheid van gras tydens die droë seisoen.

Die bevindings van hierdie studie is gebruik om kwessies rakende die bewaring van sebra in MWR te identifiseer en ‘n bewarings- en bestuursplan voor te stel.

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Chapter One

General introduction and thesis outline

1.1 Introduction

1.1.1 *Status and conservation of zebras*

Zebra occur throughout Africa and are generally one of the most abundant members of the ungulate community, playing a vital role in maintaining the overall dynamics and well-being of the habitats they occupy (Hack, East & Rubenstein, 2002). However, during the last 100 years, zebras have experienced significant population declines and range reductions. Three species of zebras persist - the Grevy's zebra (*Equus grevyi*), mountain zebra (*Equus zebra*) and plains zebra (*Equus quagga*) (Moehlman, King & Kebede, 2016). The Grevy's zebra and mountain zebra are threatened with extinction, and according to the IUCN Red List the Grevy's zebra is categorized as Endangered and the mountain zebra as Vulnerable (Novellie, 2008; Rubenstein, Low Mackey, Davidson, Kebede & King, 2016). The plains zebra was recently uplisted from Least Concern to Near Threatened (King & Moehlman, 2016).

Historically the Grevy's zebra occurred throughout the Horn of Africa, including Kenya, Ethiopia, Somalia and South Sudan (Moehlman *et al.*, 2016; Rubenstein *et al.*, 2016). At present, only small, isolated populations occur in Ethiopia and Kenya (less than 0.5% of their range are in protected areas), making it the largest range reduction undergone by any African mammal to date (Rubenstein *et al.*, 2016). Their estimated global population also declined from 15 000 animals in the 1970s to 2 837 in 2011, thus roughly an 80% decline in their global population (Kenya Wildlife Service, 2012; Moehlman *et al.*, 2016; Rowen & Ginsberg, 1992).

The decline in Grevy's zebra numbers is mainly attributed to habitat degradation and loss as a result of overgrazing of livestock, reduction of available water sources (as they are highly dependent on access to water), competition for resources, hunting and disease (Kebede, 2013; Rowen & Ginsberg, 1992; Williams, 2002, 2013). However, in both Kenya and Ethiopia there has been a small, positive increase in population numbers since the early 2000s (Moehlman *et al*., 2016).

In northern Kenya, survivorship has improved thanks to community-based conservation and the establishment of conservation conservancies (Kenya Wildlife Service, 2012; Low, Sundaresan, Fischhoff & Rubenstein, 2009). The reduction of domestic livestock competition and an increase in protection on the Laikipia Plateau has also allowed for an increase in zebra populations (Williams 2002, 2013). Yet, to advance the protection of wild Grevy's populations, Williams (2002) has suggested that several conservation actions involving the management of protected areas, protection of water supplies, community conservation and monitoring of numbers in the wild is needed.

The mountain zebra (*Equus zebra*) can be divided into two subspecies, the Cape mountain zebra (*Equus zebra zebra*) and the Hartmann's mountain zebra (*Equus zebra hartmannae*) (Moehlman *et al*., 2016; Novellie, 2008). The historical range of the Cape mountain zebra stretched from the Amatola Mountains in the Cathcart District of the Eastern Cape, to the Kamiesberg in Namaqualand, South Africa, and the Hartmann's mountain zebra occurred from southern Angola to the Namib Desert and central plateau of Namibia (Novellie, 2008; Novellie, Lindeque, Lindeque, Llyod & Koen, 2002; Penzhorn, 2013).

Between 1973 and 1989, the Hartmann's mountain zebra declined from 50 000 to 7 500 individuals (Joubert, 1973; Novellie *et al*., 2002). The major causes of the decline were restricted access to water and forage due to droughts and fencing that prevented access to resources and limited migration, combined with hunting (Novellie, Llyod & Joubert, 1992). Improved protection, establishment of artificial waterholes, and community-based and private enterprise conservation has allowed the Hartmann's mountain zebra population to recover to over 25 000 since the 1980s (Moehlman *et al*., 2016).

In contrast, by the 1950's only 30 Cape mountain zebra remained (Hrabar *et al*., 2015). However, through an extensive reintroduction program, populations of Cape mountain zebra have been re-established within their historic range (Lloyd, 2002; Novellie *et al*., 2002). Today, established populations only persist in the Mountain Zebra National Park, Kammanassie Mountains and Gamka Mountain Reserve in South Africa (Moehlman *et al*., 2016; Novellie *et al*. 2002). However, throughout South Africa they also occur on private game ranches and reserves. In 2003, the population of Cape mountain zebra was estimated to be 3 100 (Novellie, 2008). Even though the population is increasing, they are still threatened by genetic deficiencies, hybridization, habitat reduction, disease, hunting and lack of management capacity (Hrabar *et al*., 2015; Moehlman *et al*., 2016).

Lastly, the plains zebra (*Equus quagga*) - the most abundant wild equid, occurred in nearly all the countries of eastern, southern and south-western Africa before the 1990s (Hack *et al*., 2002). Since then, plains zebra have experienced many population declines and local extinctions within their range, totalling a 25% population reduction since 1992 (King & Moehlman, 2016). Yet no severe reductions have been noticed within their historic range, apart from their extinction in both Burundi and Lesotho and possibly in Somalia (King & Moehlman, 2016; Moehlman, 2002).

Even though the plains zebra is categorized by the IUCN Red List as Near Threatened, one of its subspecies, the quagga (*Equus quagga quagga*), which ranged from the Orange and Vaal River, throughout the Cape Province to west of the Drakensberg in South Africa, is categorized as Extinct (King & Moehlman, 2016; Moehlman *et al*., 2016). The Burchell's zebra (*Equus quagga burchelli*) is categorized as Least Concern, although it no longer occurs in the middle of its range and the Damara zebra (*Equus quagga antiquorum*), which is included under the Burchell's zebra, has gone extinct in the wild (Hack *et al*., 2002; King & Moehlman, 2016). The rest of the plains zebra's subspecies are listed on the IUCN Red List as follows: Crawshay's zebra (*Equus qugga crawshayi*) as Endangered; Boehm's zebra (*Equus quagga boehmi*) as Lower Risk; Chapman's zebra (*Equus quagga chapmani*) as Data Deficient and maneless zebra (*Equus quagga borensis*) as critically Endangered (Hack *et al*., 2002; King & Moehlman, 2016).

The local extinctions and declines within the plains zebra population are primarily the result of overhunting and habitat degradation due to an increase in human development and livestock conflicts (Groom & Harris, 2009). The majority of plains zebra population declines are occurring outside of protected areas (Moehlman *et al*., 2016). For example outside of protected areas in South Africa, plains zebra are at risk due to a combination of factors, including: 1) habitat loss as a result of increasing agriculture and livestock farming; 2) hunting and fencing off of zebra due to resource competition with livestock; 3) loss of genetic diversity due to small private property populations (less than 100 individuals); and 4) the spread of diseases through translocations into new regions (Stears, Shrader & Castley, 2016). The situation in South Africa is however helping management and conservation agencies to predict the future threats plains zebra might face throughout the rest of their range. Competition for land and resources will increase with the exponential increase in human population and agriculture. Fencing is likely to increase and populations will become more isolated, resulting in gene flow reduction or elimination (Moehlman *et al*., 2016).

In contrast, plains zebra are abundant within protected areas throughout the rest of their range and in the presence of successful conservation and management efforts they are still considered widespread and abundant (King & Moehlman, 2016). The continued existence of the species is also ensured by the existence of sizeable protected areas, for example the Serengeti-Mara ecosystem. The status of the plains zebra provides hope for the conservation of zebras as a whole, since it indicates that zebras can still flourish under a rising anthropogenic environment, and they also provide knowledge on the conditions that are needed to maintain sustainable zebra populations (Moehlman *et al*., 2016).

The long-term conservation of the plains zebra in a natural, free-ranging state depends entirely on their fate within East Africa, since 70% of the global population remains within this region of Africa (Hack *et al*., 2002). It is therefore of particular concern that in all but two East African countries, plains zebra populations are declining. The most alarming of these are the recent declines observed within Kenya and Tanzania, where plains zebra are most abundant. Populations appear to be stable only in Ethiopia and Malawi (King & Moehlman, 2016).

This is ironic, as Malawi is home to the smallest population of zebra within East Africa with only 748 zebra occurring in the country - all within protected areas. Majete Wildlife Reserve hosts the largest zebra population and experienced an increase from 262 to at least 571 individuals between 2012 and 2015. However, all other protected areas within Malawi have experienced a decline in populations: Nyika National Park declined from 279 to 153 between 2013 and 2015; and in 2015, Liwonde National Park, Kasungu National

Park and Vwaza Marsh Wildlife Reserve had less than 20 zebra each (King & Moehlman, 2016). However, 50 zebra were translocated from Majete Wildlife Reserve to Liwonde National Park between July 2016 and July 2017. In addition, 25 zebra were translocated from Majete to Nkhotakota Wildlife Reserve in July 2017.

To ensure the persistence of the plains zebra, Hack *et al*. (2002) proposed that along with more frequent monitoring and improved coverage of monitoring, the following conservation actions are needed: 1) improved risk assessment – especially outside of protected areas; 2) a better understanding of the basic biology of plains zebra; 3) prevention of genetic uniformity and 4) a meticulous investigation on the economics alternatives of utilization strategies. This can prove challenging as studies on plains zebra are complex when it comes to accuracy and frequency of monitoring because the species occupies an extensive range and occurs on both protected and non-protected lands (Moehlman *et al*., 2016).

Due to human intervention some zebra populations have experienced remarkable recoveries (Moehlman *et al*., 2016). For example, the Cape mountain zebra was prevented from going extinct with the help of committed management programs (Novellie, 2008). The conservation of the Hartmann's mountain zebra and Grevy's zebra has been aided by improved awareness and support of local communities and in Botswana, the removal of a veterinary corridor fence allowed the plains zebra to resume migration (Bartlam-Brooks, Bonyongo & Harris, 2011; King & Moehlman, 2016; Rubenstein *et al*., 2016). Thus the conservation of zebras is highly dependent on the continued commitment of wildlife conservation authorities, researchers and local communities (Moehlman *et al*., 2016).

1.1.2 *Reintroductions of wild zebras*

Increasing human populations have resulted in roads, railroads and fences fragmenting large ecosystems. The fragmentation of ecosystems can have detrimental effects on zebra populations and other large ungulates (Ogutu, Owen-Smith, Peipho & Said, 2011). Fencing, agriculture and domestic livestock can also reduce zebra's access to water and forage, affecting their survival and reproduction rates (Moehlman *et al*., 2016). As a result, populations have become more saturated and subpopulations permanently isolated. Thus, successful conservation efforts are now dependent on reintroductions to reinforce populations or to maintain genetic variability (Kaczensky *et al*., 2016).

Reintroductions can be defined as the: “human-assisted movement of animals among small, isolated populations managed as one metapopulation, with the aim to reinforce population size or enhance or maintain genetic variability” (Hrabar & Kerley, 2013). Initially, reintroduction projects were initiated when little information of the respective species’ ecological or spatial requirements were available. However, thanks to scientific research and experience with animal reintroductions, reintroductions have significantly advanced since then; in 1988 the Reintroduction Specialist Group of the International Union for the Conservation of Nature Species Survival Commission (IUCN/SSC) was founded. Today all reintroductions are planned, implemented and evaluated according to the “Guidelines on Reintroduction and Other Conservation Translocations” as established by the IUCN/SSC (Kaczensky *et al*., 2016).

The guideline requirements according to the IUCN/SSC (2013) include: 1) a comprehensive justification; 2) a detailed risk assessment of the translocation; 3) the translocation’s viability and design must integrate social, economical and political factors; 4) once the translocation is in progress, the design and operation should follow the standard steps of project design and management and 5) the translocation must be thoroughly documented and the results must be made publicly available for future conservation planning.

Even though guidelines are provided, reintroductions can be logistically challenging, costly and require long-term commitment (IUCN/SSC, 2013). Reintroductions can also influence the well-being and reproductive potential of the reintroduced individual, and even lead to death (Harrington *et al*., 2013; Letty, Marchandeau & Aubineau, 2007). Setbacks should be expected, especially if the original cause of extinction has not yet been established and if the founding population is small. Special care must also be taken to prevent that reintroductions divert the necessary funds, attention and efforts away from conserving the last indigenous population. Reintroductions should therefore be viewed as a last resort and conserving wild zebras and their habitat should always be given priority (Kaczensky *et al*., 2016).

Reintroductions have played a variable role in the conservation and management of the three zebra species (Kaczensky *et al*., 2016). Reintroductions have had a significantly large impact on the conservation of the Cape mountain zebra and saved the species from extinction (Hrabar & Kerley, 2013; Novellie *et al*., 2002). In contrast, no introductions of Grevy's zebra have taken place to date, but small populations of the species have been reinforced (Kaczensky *et al*., 2016). For example in 2002, the remaining population of two individuals in Meru National Park was supplemented with thirteen individuals (Franceschini, Rubenstein, Low & Romero, 2008). Numerous reintroductions of plains zebra have also taken place, in particular in southern Africa, as many game ranches have relied on translocation to return plains zebra to areas where farming had resulted in their local extinction (Hack *et al*., 2002).

Within Majete Wildlife Reserve (MWR), located in southern Malawi, high levels of poaching and a lack of law enforcement lead to the local extinction of zebra as well as other large mammals within the reserve and surroundings by 1985 (Patton, 2011). In 2003, African Parks Majete (Pty) Ltd., together with the Malawian government's Department of National Parks and Wildlife (DNPW), entered into a public-private partnership (PPP), through which they aimed to rehabilitate the reserve (Wienand, 2013). Between 2004 and 2009, 174 plains zebra (*Equus quagga*) were reintroduced to the reserve from game ranches throughout Zambia, as well as from Liwonde National Park, Malawi (Appendix 1.1) (A. Uys & P. Ndadzela, personal communication, February 2, 2017). According to the most recent aerial survey conducted in 2015, Majete's zebra population stands at at least 571 individuals. Due to the successful reintroduction and establishment of plains zebra within Majete, 23 zebra were translocated from MWR to Liwonde National Park, Malawi, during July 2016. In July 2017, an additional 27 zebra were translocted to Liwonde, as well as another 25 to Nkhotakota Wildlife Reserve, Malawi (Appendix 1.2).

Though zebra have been successfully reintroduced and established in MWR – thanks to their remarkable ability to recover when provided with suitable habitat and protection from overhunting; it is important to investigate and monitor the period after reintroduction, as population dynamics, distribution and behaviour may show discrepancies as species adapt and establish in their new environment (King &

Moehlman, 2016; Sarrazin & Barbault, 1996). In order to ensure that management and conservation agencies continue to advance the long-term persistence of the plains zebra, and to understand how they will respond to future human-induced changes, a thorough investigation into the ecology of reintroduced plains zebra is needed (Hack *et al.*, 2002).

In Malawi, numerous conservation measures involving the reintroduction of zebra into extirpated or previously saturated areas are also ongoing - the African Parks Network has recently included Liwonde National Park and Nkhotakota Wildlife Reserve in their management portfolio, the International Fund for Animal Welfare (IFAW) is funding an anti-poaching project in Kasungu National Park with the possibility of expanding Kasungu National Park into a trans-frontier park with Likusuzi National Park and Luambe National Park in Zambia; and a Nyika Trans-Frontier Project (including Nyika National Park and Vwaza Marsh Wildlife Reserve in Malawi and Musalangu Game Management Area, Mitenge Forest Reserve and Lundazi Forest Reserve in Zambia), which is run by the DNPW of Malawi, is in progress (King & Moehlman, 2016).

The current study will therefore provide fundamental information on how the Majete reintroduction has performed, provide insights into future reintroduction projects, and enhance our knowledge on how pioneer zebra populations establish themselves (Sarrazin & Barbault, 1996). Lastly, it will also improve our understanding on how zebra are limited by or exploit their natural resources, which will help managers better understand zebra carrying capacity of MWR (Sarrazin & Barbault, 1996).

1.2 Focal species

Plains zebra occur throughout southern and eastern Africa and are characterized as a wild African equid with distinct black and white stripes (Kingdon, 2004; Stuart & Stuart, 2007). They have an average shoulder height of 1.3m and adults can weigh between 290 - 340kg (Hack *et al.*, 2002; Stuart & Stuart, 2007).

Plains zebra can be divided into six morphologically distinct subspecies, namely: Boehm's zebra (*Equus quagga boehmi*), Crawshay's zebra (*Equus qugga crawshayi*), Chapman's zebra (*Equus quagga chapmani*), Burchell's zebra (*Equus quagga burchelli*), maneless zebra (*Equus quagga borensis*) and quagga (*Equus quagga quagga*) (King & Moehlman, 2016). Subspecies are differentiated by a variation in body size, stripe width and stripe pattern (Brooks, 2005; Hack *et al*., 2002). In general, body size and stripe width decreases from south to north, by approximately 28 - 40% and in contrast, the extent of their stripe pattern coverage increases from south to north (Hack *et al*., 2002; Smuts, 1975). Subspecies can also be separated by small differences in cranial and tooth characters (Groves & Willoughby, 1981), but genetic differentiations between the subspecies are very small (Lorenzen, Arctander & Siegismund, 2008).

Plains zebra are pure grazers and are strongly associated with grasslands, savannas and open-grassed woodlands (Kingdon, 2004). They can be found in these habitats in tropical and temperate climates and from sea level to over 3,500m in elevation. Only deserts, dense forests and permanent wetlands are avoided (King & Moehlman, 2016). Unlike other African savanna antelope and ruminants which also graze purely on grass, the plains zebra make use of a hind-gut digestive system which enables them to digest their food at a comparatively faster rate (Hack *et al*., 2002). This allows them to graze on coarse vegetation of low nutritional value, which is unsustainable for similar sized ruminants (Brooks, 2005; Duncan, Foose, Gordon, Gakahu & Lloyd, 1990). The ability to survive on low quality forage has enabled the plains zebra to exploit a greater range in grass quality, and thus plains zebra are able to occupy a wider variety of habitats and geographical ranges than most other similar sized ungulates (Hack *et al*., 2002). It also enables the species to undergo large migrations to track changing resources and to facilitate the grassland to more selective ruminants. For example, by removing the older growth, zebra open up the nutritious new growth to wildebeest (*Connochaetes*) and Thompson’s gazelle (*Eudorcas thomsonii*) (Bell, 1971; Owaga, 1975; Owen-Smith, 1988; Vesey-Fitzgerald, 1960).

Regarding the social structure of plains zebra, a two-tiered social organization has been reported (Hack *et al*., 2002; Simpson, Rands & Nicol, 2012). Firstly, the family band – consisting of a single stallion and one to six females and their foals; form the core social group (Fischhoff, Sundaresan, Cordingley & Rubenstein, 2007; Klingel, 1969; Pluhácek & Bartos, 2005). Harems (the females and foals of a band) are generally stable, consisting of the same adult members for several months to years (Fischhoff, Dushoff, Sundaresan, Cordingley & Rubenstein, 2009). It is the responsibility of a harem stallion to defend all the members of the harem and a stallion's tenure can last up to 10 years (Hack *et al*., 2002; Pluháček & Bartos, 2005). Older males who have lost their harems to a rival male, and young males who have recently dispersed from their natal harems, aggregate to form bachelor groups of up to 50 individuals (Hack *et al*., 2002; Klingel, 1969). Young females that have dispersed from their natal harems may alternate between three to four harems before settling (Boyd, Scorolli, Nowzari & Bouskila, 2016). Additionally, multiple bands and bachelors can merge to form larger herds (Fischhoff *et al*., 2009).

A twelve-month gestation period has been documented for plains zebra, after which one foal is usually born. Foals generally suckle milk for up to six months, but can start grazing within the first month. They reach sexual maturity at the age of two years, however females tend to cycle without conceiving for one to two years after reaching sexual maturity and males generally only acquire harems after the age of five (Kingdon, 2004). Plains zebra can live to the age of 23 years (King & Moehlman, 2016; Ransom *et al*., 2016).

1.3 Study site

Majete Wildlife Reserve is located in the Lower Shire Valley region of southern Malawi and covers 700km^2. The climate is characterized as semiarid and can be categorized into three main seasons based on temperature and rainfall: the hot wet season (mid November to April), the cold dry season (May to August) and the hot dry season (September to mid November) (Gyöngyi, 2011; Sherry, 1989). The average daily temperature is 28.4°C in summer (December to February) and 23.3°C in the winter (June to August) (Spies, 2015; Wienand, 2013). The expected annual rainfall in the eastern parts of the reserve ranges between 680 - 800mm and in the west, between 700 - 1000mm (Gyöngyi, 2011; Spies, 2015).

The western region of the reserve is characterized by rolling hills and the terrain decreases in altitude and becomes more level progressing eastwards. The highest point of the reserve stands at 766m (Majete Hill) and the lowest point at 100m (Kapichera Falls located in the Shire River) (Bell, 1984). The eastern border of the reserve runs along 12km of the Shire River and the only other perennial river that cuts through the reserve is the Mkulumadzi River (Figure 1.1). A number of small seasonal rivers flow toward the Shire

River from a NW to SE direction. These small perennial rivers include the Nsepete, Nakamba, Mwambezi, Milassi, Masakhala, Nthumba and Kakoma (Sherry, 1989). Seven perennial springs are found within the reserve, and numerous ephemeral pools occur during the wet season. Ten artificial water points (AWPs) were also created within the reserve to account for the lack of permanent water bodies – especially since water is extremely scarce in the dry season (Bell, 1984; Chamaillé-Jammes, Fritz & Murindagomo, 2007; Gyöngyi, 2011; Wienand, 2013).

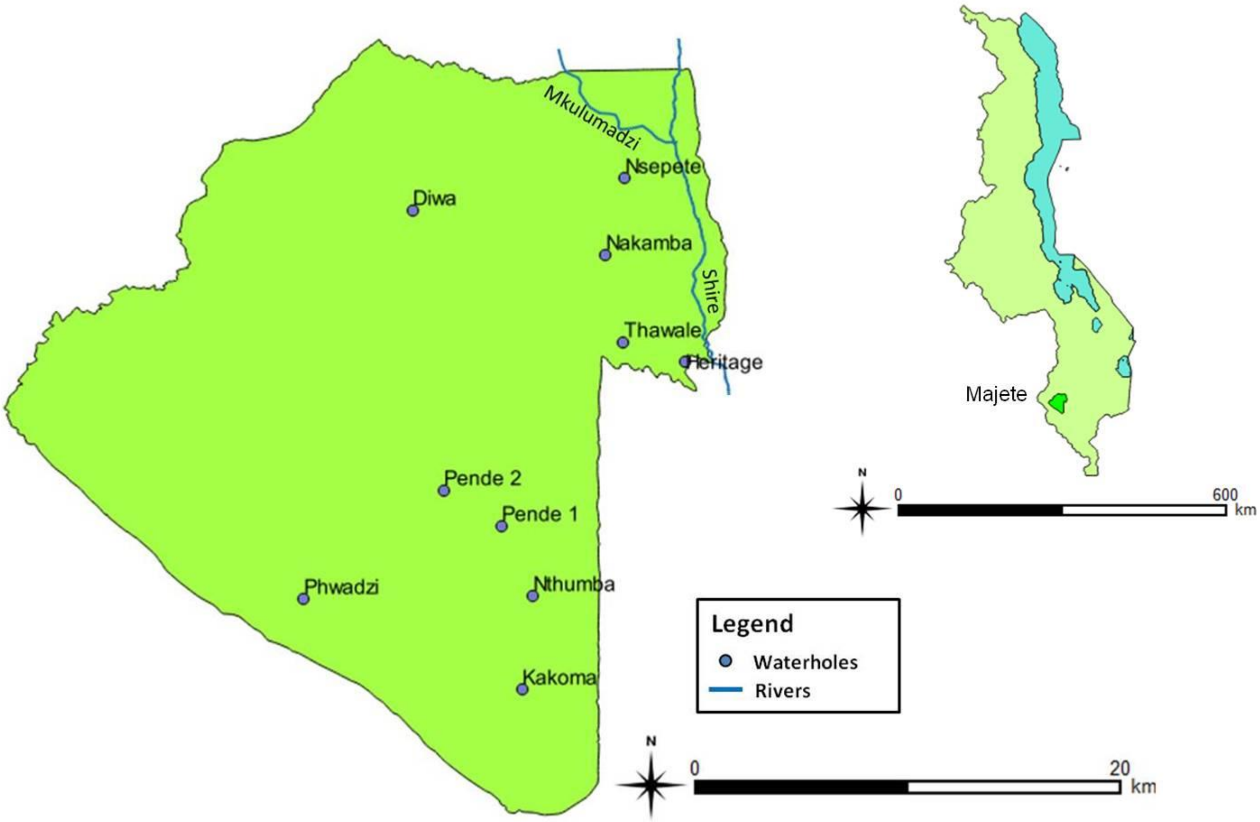

Figure 1.1 The position of Majete Wildlife Reserve in Malawi; and the location of the ten AWPs (artificial water points) and two perennial rivers that occur in Majete Wildlife Reserve (Shapefiles pers. comm. African Parks (Pty) Ltd.)

The vegetation classes of Majete are strongly associated with soil type and depth, however they are often combined and difficult to successfully classify. The soil composition can be defined as mainly lithosols, including either shallow, stony, ferruginous soils or sandy and loamy soils (Sherry, 1989; Spies, 2015). The western region of the reserve has relatively deep red clay loams and the eastern region, shallower and sandier loams (Bell, 1984). Limited deposits of alluvial soil can be found along some of the rivers (Sherry, 1989; Spies, 2015). Sherry (1989) classified the vegetation types into: riparian thicket (1%), riverine and alluvial associations (12%), low altitude mixed deciduous woodland (30.7%), ridge-top mixed woodland (7.2%), medium altitude mixed deciduous woodland (16.8%) and high altitude miombo woodland (32.3%). A more recent vegetation study, conducted in 2015, found that the vegetation of MWR is mainly miombo savanna woodland. Miombo savanna woodland is the most extensive woody savanna formation of Africa (covering approximately 2.7 million km^2) and is dominated by trees in the genera *Brachystegia*, *Julbernardia* and *Isoberlinia*, as well as an underlying layer of grass (Mwase, Bjørnstad, Bokosi, Kwapata & Stedje, 2007). The miombo savanna woodland in MWR can be classified into four distinct vegetation classes: low altitude mixed woodland (below 250m), medium altitude mixed woodland (250 - 400m), high altitude miombo woodland (over 400m) and savanna (Figure 1.2: African Parks Majete (Pty) Ltd., personal communication, March 21, 2016). The low altitude mixed woodland is characterised by *Acacia* species and *Steculia*, medium altitude mixed woodland by *Brachystegia boehmii, Diiospyrus kirkii* and *Combretum* species, high altitude mixed woodland by *Brachystegia boehmii, Burkea africana* and *Pterocarpus* and savanna by *Combretum* species*, Acacia* species and *Panicum* species (Forrer, 2016). This more recent vegetation study still needs to be ground-truthed (C. Hay, personal communication, March 21, 2016).

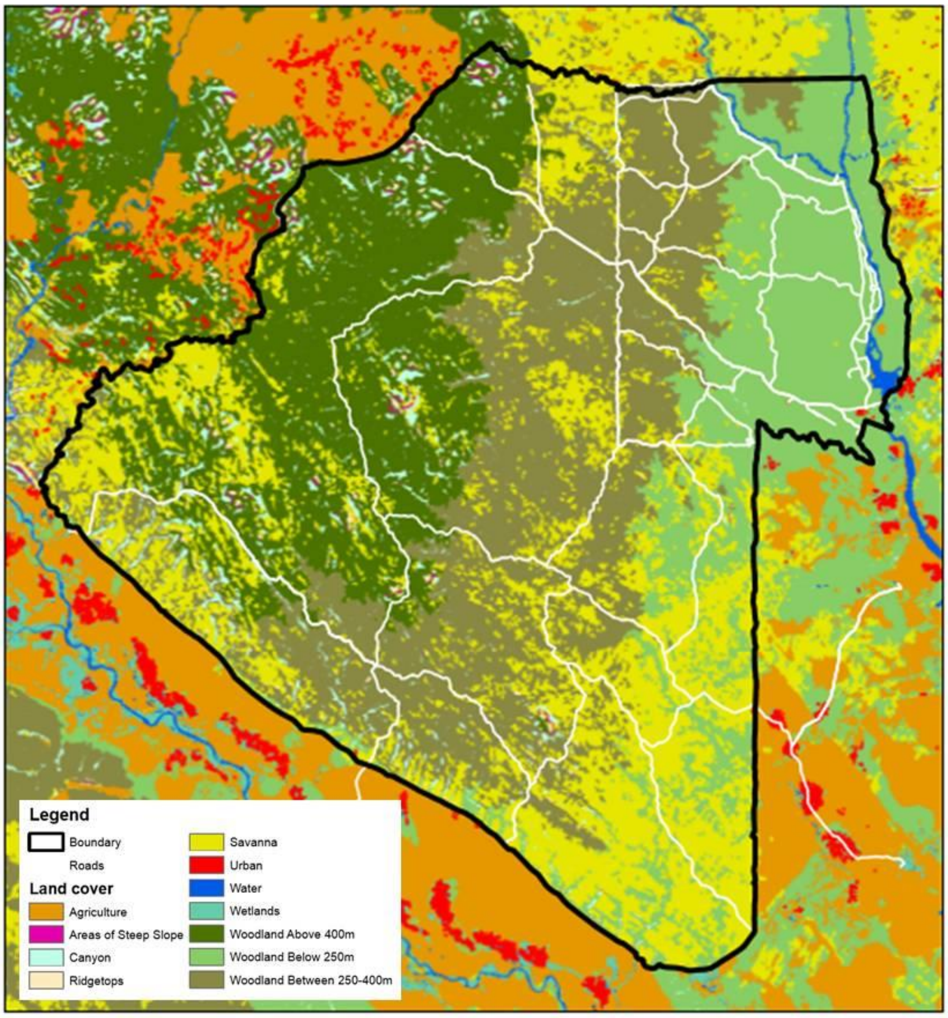

Figure 1.2 A vegetation map of Majete Wildlife Reserve and its surroundings (supplied by African Parks Majete (Pty) Ltd., 2016)

In 1951, MWR was declared a non-hunting area to prevent the declines in large mammal species, as well as human encroachment (Morris, 2006). In 1955, it was proclaimed a game reserve and was extended in 1969 to include an additional kilometer of the Shire and the Mkulumadzi Rivers (Gyöngyi, 2011; Sherry, 1989). By the mid-1990s most large mammals were completely eradicated from MWR due to high levels of local and cross-border poaching as a result of the Mozambican civil war, illegal logging and charcoal production, as well as a lack of law enforcement, poor management and insufficient resources (Gyöngyi, 2011; Morris, 2006). This all changed in March 2003 when the 25-year PPP was established (Wienand, 2013). Since then Majete's infrastructure has been developed, 12 herbivore species and 6 leopards and 3 lions were reintroduced (over 2550 animals; Appendix 1.1), law enforcement was re-established and partnerships providing community support developed (Gyöngyi, 2011; Wienand, 2013). However, illegal charcoal production is still a problem in areas surrounding the reserve (Gyöngyi, 2011).

In 2003, only the Sanctuary (a 14 000ha site located in the north-eastern region of the reserve) was fenced and used for wildlife reintroductions. The remainder of the reserve was completely fenced by 2008 and in May 2011, the sanctuary fence was removed and wildlife was reintroduced into the rest of the reserve (Gyöngyi, 2011; Wienand, 2013). It is important to note that prior to 2003, no fire management took place in the reserve and since then an effort has been made to practice prescribed controlled burns and to reduce wildfires (Wienand, 2013).

According to the most recent aerial survey conducted in 2015, MWR has over 13 000 animals (C. Hay, personal communication, February 1, 2017). Currently, no culling or hunting is allowed in the reserve, with the aim to replenish other protected areas within Malawi by relocating surplus animals (Appendix 1.2) (Forrer, 2016).

1.4 Research goal and objectives

1.4.1 *Goal*

To provide guidelines for Majete Wildlife Reserve on zebra management and conservation based on ecological and scientifically sound research; as well as to provide guidelines for future zebra reintroductions in Malawi. These guidelines will aim to incorporate demographics, behaviour, waterhole usage and dietary requirements related to the plains zebra.

1.4.2 *Objectives and research questions*

1. To determine if reintroduced plains zebra in MWR have established, organised, and distributed themselves more than ten years after their initial reintroduction within the same general structure as found in established populations, and if not what are influencing these differences. Specifically, we aim to determine:

   1.1 The direction and magnitude of population growth
   1.2 The sex ratio of adult zebra in MWR
   1.3 The range and average size of MWR's zebra bands
   1.4 The average age class and sexual composition of zebra bands
   1.5 If plains zebra stallions form bachelor groups in MWR, and if so determine the range and average size
   1.6 Determine if zebra bands are stable or dynamic in composition.
   1.7 If bands and bachelor groups merge to form temporary herds in MWR, and if so determine the average size.

2. To determine how plains zebra in MWR utilise browse and graze in their diet based on isotope composition of C_3 and C_4 biomass consumed, how this may vary between seasons, and what implications such dietary choices have in resource availability and use.

3. To determine the extent to which plains zebra utilise artificial waterholes in MWR and to quantify factors associated with those use patterns. Specifically, we aim to determine:

   3.1. What frequency and time of day zebra use artificial waterholes
   3.2. If there a seasonal variation in the utilization of artificial waterholes
   3.3. If zebra interact more with certain species at artificial waterholes, and if so determine if such interactions are competitive or neutral and why. Specifically, to determine if artificial waterhole interactions are influenced by species, group size of the initiating species, unit mass of the initiating species, group mass of the interacting species, group size of the zebra being interacted with, band composition (family or bachelor group) of the zebra group and/or the different seasons.

4. To determine if reintroduced plains zebra in MWR allocate their time similarly to established populations and if not, can the differences be explained by environmental, demographic, or resource-driven factors. Specifically, we aim to determine:

4.1. How plains zebra allocate their daylight time budget among feeding, resting, locomotion, standing attentive, maintenance and social behaviour, and to what extent season, time of day, band composition, group size, sex, body composition, and age influence those parts of the compositional budget.

4.2. The frequency of social interactions between plains zebra within their family and bachelor bands and if these rates are comparable to those found in established populations.

1.5 Thesis structure

This thesis consists of six chapters, of which four of the Chapters (Chapter Two, Three, Four and Five) have been compiled in the format of stand-alone manuscripts. This specific format has been selected to assist with publication in peer-reviewed journals. Therefore, a degree of repetition and cross-referencing between chapters occurs.

After a general introduction of the status and conservation of zebras, reintroductions of wild zebras, study species, study site, research goals and objectives in Chapter One; Chapter Two describes the demography and distribution of plains zebra within MWR.

Chapter Three investigates the diet of plains zebra. Stable isotope analysis was used to determine the C_3 and C_4 biomass within their diet and seasonal dietary variation. The dietary preference of plains zebra is discussed in light of the study’s findings.

Chapter Four elaborates on artificial waterhole usage by the zebra of Majete. It also describes seasonal variation within artificial waterhole usage, as well as the rate of interactions between zebra and other species around artificial waterholes. This is followed by a discussion regarding zebra and artificial waterhole management.

In Chapter Five, the time budget and social interactions of plains zebra are determined using behavioural ethograms. Chapter Six summarizes the results and conclusions of the study and proposes recommendations for the management of zebra within MWR, as well as future reintroductions within the rest of Malawi.

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Chapter Two

Demography and social organization of reintroduced plains zebra (*Equus quagga*) within Majete Wildlife Reserve, Malawi

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2.1 Abstract

This study aimed to quantify the demography and social organization of plains zebra in Majete Wildlife Reserve (MWR) more than ten years after their initial reintroduction, with the use of driving transects, camera traps and aerial surveys. A total of 243 unique individuals were indentified (roughly 40% of the population), of which 168 were adults (69.1%) with a sex ratio of 0.8:1.0 (male:female), 32 were yearlings (13.2%) and 43 were foals (17.7%). Family band size varied from two to eleven individuals (mean = 6.3 ± 0.21 [SE]) and each band was comprised of a single adult male with one to five adult females (mean = 2.8 ± 0.10), zero to three yearlings (mean = 0.6 ± 0.09) and zero to four foals (mean = 1.5 ± 0.11). Bachelor groups ranged from one to eight males (mean = 3.0 ± 0.21) and were significantly less stable than family groups. The formation of herds (multiple bands associating with each other) was never observed in MWR. The MWR zebra population appears to be successfully establishing, with structure and organization similar to some established populations. Sex ratio and composition of the founding population, as well as environmental factors may explain some differences when compared to established populations. Active management and monitoring is still needed as this population continues to grow towards carrying capacity since resource availability

will fluctuate over time and the small predator population currently present within MWR will continue to increase and eventually affect the zebra population. More precise measures of population growth is needed and will require surveys that employ statistical sampling techniques, which will in turn allow more robust population modelling and deeper understanding of the dynamics at work for zebra at Majete.

2.2 Introduction

With the changing climate and drastic expansion of the human population, the incorporation of demographic knowledge into conservation efforts will be one of the most important tools towards reducing the destructive effects of habitat fragmentation and competition for resources (King, Asa, Plucháček, Houpt & Ransom, 2016). Understanding the organization of animals can also be of significant value when dealing with a species' influence and position in an ecosystem; and it can improve our knowledge of how groups function and individuals react (Ransom & Cade, 2009; Rubenstein, 2010). Animal demography and organization can also inform management about the welfare of the species (King *et al.*, 2016). Thus, comprehending the demography and social organization of a species is essential for future conservation and management (Boyd, Scorolli, Nowzari & Bouskila, 2016). Numerous studies have been conducted on the demography and organization of plains zebra (*Equus quagga*) in established populations (Fischhoff *et al.*, 2007; Fischhoff, Dushoff, Sundaresan, Cordingley & Rubenstein, 2009; Gasaway, Gasaway & Berry, 1996, Goargiadis, Hack & Turpin, 2003; Klingel, 1969; Rubenstein, 1994, 2010; Rubenstein & Hack, 2004). However, very few studies have examined the demographics of plains zebra after reintroduction.

Plains zebra are gregarious and typically have a harem-forming social organization with female defence polygyny (Boyd *et al.*, 2016; Hack, East & Rubenstein, 2002; Simpson *et al.*, 2012). The core social group, known as a band, is generally comprised of a single adult male (who is responsible for defending the harem members) and one to six adult females and their foals (Boyd *et al.*, 2016; Fischhoff *et al.*, 2007; Hack *et al.*, 2002; Klingel, 1969; Pluhácek & Bartos, 2005). Observed band size for this species ranges between two and sixteen (Boyd *et al.*, 2016). Bands are generally stable and lifelong social bonds have been observed between adult females residing in the same harem until death, yet quantification of such social bonds is still needed (Boyd *et al*., 2016; Fischhoff *et al*., 2009; Klingel, 1975; Penzhorn, 1984). Young females disperse from their natal bands and may move among three to four bands before settling (Boyd *et al*., 2016).

Males obtain their own harem from the age of five years old and their tenure can last up to ten years (Boyd *et al*., 2016; Klingel, 1969; Penzhorn, 1984; Pluháček & Bartos, 2005). A male can attain its own harem by abducting a harem from another male or by taking over a harem when the previous male (the band stallion) dies (Hack *et al*., 2002; Pluháček & Bartos, 2005). Stallions who have lost their harems to a rival male or who have recently dispersed from their natal bands, can either be solitary or aggregate to form bachelor groups of up to 50 individuals (Hack *et al*., 2002; Klingel, 1969, 1974, 1975; Rubenstein, 1986). However, bachelor groups generally only consist of three males and tend to be unstable – with bachelor core groups lasting only a few months or years (Linklater, 2000).

Multiple bands and bachelors can unite to form larger herds (Fischhoff *et al*., 2009). One of the largest herds observed included over 400 individuals from as many as 100 bands (Rubenstein & Hack, 2004). Plains zebra may form herds to reduce predation risk, to gain shelter from harsh climatic conditions and/or to avoid the harassment of females by bachelors (Boyd *et al*., 2016; Rubenstein, 1986, 1994; Rubenstein & Hack, 2004). However, in relation to a change in ecological pressures (the availability of food and water or the risk of predation), the group size of both herds and bands will also vary (Rubenstein, 1986). Even though group size may vary, it has been found that unmanaged plains zebra generally have a sex ratio of 1:1 (Boyd *et al*., 2016).

Although the demography and organization of wild plains zebra have been well examined, research conducted on reintroduced plains zebra are still limited and there is a need to improve our knowledge on how pioneer plains zebra populations establish and organize themselves in their reintroduced habitat (Kaczensky et al., 2016; King & Moehlman, 2016; Sarrazin & Barbault, 1996). Reintroductions can be defined as the: "human-assisted movement of animals among small, isolated populations managed as one metapopulation, with the aim to reinforce population size or enhance or maintain genetic variability" (Hrabar & Kerley, 2013). Today, the "Guidelines on Reintroduction and Other Conservation Translocations" (founded by the IUCN/SSC) are used to plan, implement and evaluate all reintroductions (Kaczensky *et al.*, 2016). However, reintroductions can be challenging both logistically and financially and can have negative consequences on the reintroduced animal (IUCN/SSC, 2013, Harrington *et al.*, 2013). In addition, long-term commitment and monitoring is needed after reintroduction because population dynamics, behaviour and distribution may change as species establish in their new habitat (King & Moehlman, 2016; Sarrazin & Barbault, 1996).

Majete Wildlife Reserve's reintroduction programme of 174 plains zebra between 2004 and 2009 presents an opportunity to carry out long-term monitoring of reintroduced plains zebra and better understand the drivers of the management action's success or failure. Furthermore, to ensure the sustainability of the reintroduced plains zebra population, active monitoring and management is also needed, since resource availability will fluctuate over time and the small predator population currently present within MWR will continue to increase and eventually effect the zebra population (Newmark, 2008). The aim of this study was to quantify the demography and organization of plains zebra in Majete Wildlife Reserve (MWR) more than ten years after their initial reintroduction. Our primary objective was to determine if the plains zebra population has established in MWR ten years post-reintroduction, and if their social organization did not differ significantly to that of other populations in eastern and southern Africa. The findings of this chapter will be taken into consideration when providing management strategies and recommendations, and have the potential to enhance our understanding of wild plains zebra reintroductions.

2.3 Methods

2.3.1 *Study site*

Located in the Lower Shire Valley region of southern Malawi, Majete Wildlife Reserve (MWR) covers 700km^2 that is characterized by rolling hills in the west and decreases in altitude towards the east. The eastern and northern border of the reserve runs along sections of either the Shire River or Mkulumadzi River, which are the two main perennial rivers located within Majete. There are also a number of small seasonal rivers, perennial springs, temporal pools and ten artificial waterholes (Forrer, 2016; Sherry, 1989; Wienand, 2013). The vegetation is mainly miombo savanna woodland, but can be divided into four distinct classes: low altitude mixed woodland, medium altitude mixed woodland, high altitude miombo woodland and savanna (Forrer, 2016).

The climate is classified as semiarid and MWR has an average rainfall of 680 - 1000mm a year (Gyöngyi, 2011; Spies, 2015). Four main seasons have been identified: the early wet season (December to February), the late wet season (March to May), the early dry season (June to August) and the late dry season (September to November) (Gyöngyi, 2011; Sherry, 1989). In the winter (June to August) the daily temperature averages at 23.3°C and at 28.4°C in the summer (December to February) (Gyöngyi, 2011; Spies, 2015; Wienand, 2013).

Even though MWR was proclaimed a non-hunting area in 1951 and gazetted into a game reserve in 1955, it was eradicated of almost all large game by the mid-1990s due to high levels of poaching and a lack of management (Gyöngyi, 2011; Sherry, 1989). In 2003, a public private partnership (PPP) was established between African Parks Majete (Pty) Ltd. and the Malawian Department of National Parks and Wildlife (DNPW) in which they aimed to commence one of Africa’s largest wildlife reintroductions and restore Majete. Initially a 140km^2 area, known as the Sanctuary, located in the north-eastern corner of the reserve, was fenced and used for the first set of wildlife reintroductions. In 2008, the remainder of the reserve was completely fenced and in 2011 the sanctuary fence line was removed. In total over 2550 animals from 14 different mammal species were reintroduced between 2003 and 2010, including 174 individual plains zebra from Liwonde National Park, Malawi, and Zambian game ranches (A. Uys, personal communication, February 2, 2017; Forrer, 2016; Spies, 2015; Wienand, 2013). There are no records of the sex and age ratio of zebra reintroduced; however, a focus was made on family groups rather than bachelors, which would imply a strongly female-biased sex ratio among the 174 founders (C. Hay and K. Vickery, personal communication, October 3, 2017).

2.3.2 *Identification and monitoring*

Driving transects were conducted from March 2016 to May 2017, at an average speed of 20 kilometres per hour on established roads throughout MWR to identify and monitor the reserve’s plains zebra (hereafter referred to as zebra) population. Sampling was conducted randomly between sunrise and sunset in order to sample each road during different times of the day. Sampling was conducted on a weekly basis within the Sanctuary and on a monthly basis within the rest of the reserve, due to logistics and because the majority of MWR's roads are located within the Sanctuary. Generally two observers were present during the sampling, however between June and December 2016 volunteers assisted with the sampling. Sampling was always conducted in the presence of a professional wildlife researcher in order to verify that accurate recordings were made. The initial detection of zebra was conducted with the naked eye and if necessary binoculars were used to determine the age class and sex of individuals. Due to the dense nature of MWR's vegetation, observations were never performed from further than 150m.

On encountering a zebra group, the observers' first responsibility was to document the group composition (number of individuals, sex and age class) and GPS location (which was used to determine the distribution of Majete's zebra, along with the data obtained from camera trapping and an aerial survey). The sex was determined by examining the genitals of each individual zebra. The age class of each zebra was estimated by comparing the relative size and proportion of each member with that of an adult zebra as described by Klingel (1969) and Grange (2006). Zebra were then classified into one of three age categories: foals (0 - 12 months), yearlings (12 - 24 months) and adults (over 2 years old). This provided information to calculate the band size (number of individuals within a band), band composition (number of males and females within a band, as well as the number of foals, yearlings and adults), bachelor organization (number of males forming a bachelor band) and the sex ratio of MWR's zebra.

Thereafter, each group of zebra was photographed (using a Canon D700 DSLR camera) as a whole and individually from both sides. Zebra were photographed individually in order to identify each animal based on the variation in their stripe pattern. By the end of the study each zebra was photographed at least once, since zebra groups were generally encountered more than once in the 15 month time period. A database containing the GPS location of individual photos of each zebra, as well as their sex, age when first spotted (including the date of the individual's first record) and their original band and band changes (with the dates when first noticed) was developed. This database was subsequently used to visually identify each individual and the individual bands in the field as the study progressed (Appendix 2). This allowed us to evade potential misidentification. Once each individual zebra was identified, group photos were used to determine band and bachelor group stability (the number of times an adult was noticed missing from its original group or the addition of a new adult member). Band stability was measured by only taking adult members into account in order to account for a seasonal variation in the production of foals. On re-encountering a previously identified zebra group, known movements of adult members were recorded. The folder was also used to determine whether harems and/or bachelor groups joined together to form herds and if so, how many individuals were in a herd, as well as how many bands.

2.3.3 *Camera trapping*

Camera trapping was used in this study to allow for the continuous monitoring of sites that due to logistic difficulties and time constraints could not be accessed on a weekly basis, and to increase the sampling area to include sites that could not be accessed by road. Camera trapping took place from August to November 2016 and 96 camera trap stations were established (Figure 2.1). The 700km^2 that makes up MWR was divided into four separate camera grids that were each sampled for a period of 20 days. In total the sample period was 88 days, which is within the recommended time period to satisfy the assumption of population closure (Karanth & Nichols, 2002). The four camera grids were based on the road network of the reserve, as well as the difference in vegetation type and altitude. Camera trap stations were located approximately 2.5km apart from each other in such a way as to cover the entire reserve. Cameras were set up at wildlife trails, jeep track intersections or in river beds. Before securing a single Cuddeback^{TM} Ambush©, Cuddeback^{TM} Attack©, Cuddeback^{TM} CE© or Bushnell^{TM} camera to a tree or shrub, cameras were set to the correct time and date; as well as to take photos at one minute intervals after being activated by motion sensors. The location of each camera trap station was recorded with a GPS eTrex® 30 (Garmin International, Olathe, KS, USA). Camera traps were used to determine the distribution of zebra within MWR and individual zebras were identified from photos as described above.

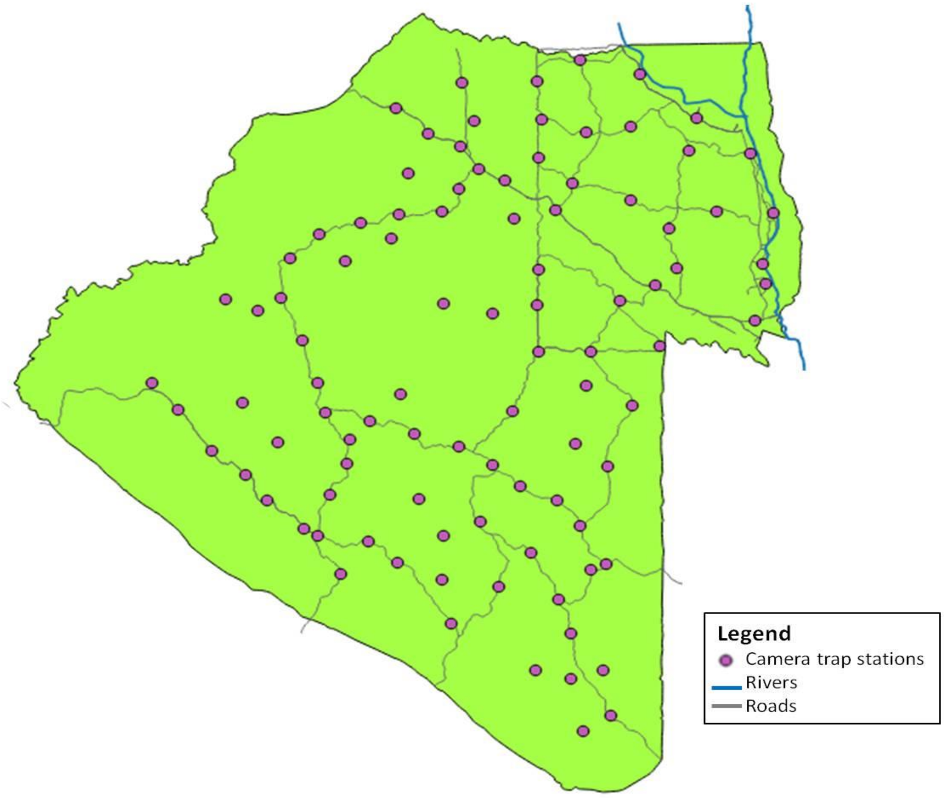

Figure 2.1 The distribution of 96 camera trap stations throughout Majete Wildlife Reserve, as well as the road network and the two main perennial rivers within the reserve (Shapefiles pers. comm. African Parks (Pty) Ltd.)

2.3.4 *Aerial survey*

An aerial survey was conducted from 21 - 23 September 2015 using a Bell 407 helicopter (Bell Helicopters, 2014) in order to determine the total population numbers of all large mammal species within MWR. The aerial survey team consisted of one pilot and three observers and the survey was conducted using transects orientated from east to west and spaced 500 meters apart, according to the recommendations of Jachmann (2002). The calibrated height above ground level was between 106 and 139 meters and a speed of less than 100 knots were maintained. The MWR was divided into three counting blocks that were surveyed on three consecutive days - due to the reserve's size making it impossible to conduct a complete survey within a single day. When animals were sighted, the observers were responsible for documenting the GPS track log of all transects, species sighted, number of individuals and the waypoint. The aerial survey zebra data for this specific study were provided by African Parks (Pty) Ltd. and used to determine the distribution of zebra within MWR.

2.3.5 *Statistical analysis*

Statistica, version 13.2 (Dell Software, 2016) was used to perform all statistical analyses. A Mann-Whitney U-Test (at the ordinal level) was conducted to determine if there was a significant difference between the stability (the number of times an adult member was noticed missing from its original group and sighted occurring with a different group or the addition of a new adult member to the original group) of bachelor and family groups. Bachelor (n = 35) and family (n = 59) groups were monitored between March 2016 and May 2017 to determine their stability and a Mann-Whintney U-Test was used as data had a non-parametric distribution (Shapiro-Wilk's test: $W = 0.61$, $p < 0.001$). The stability of only adult members was investigated in order to account for the seasonal variation in the production of foals. A simple linear regression was used to determine if there was a significant relationship between the band size and the relative number of foals (the number of foals divided by the number of adult females per band), as well as the band size and the relative number of foals and yearlings (the number of foals and yearlings divided by the number of adult females per band). QGIS, version 2.14.0 (Quantum GIS Development Team, 2014) was used to construct the distribution map of plains zebra within MWR and the shapefiles were provided by African Parks (Pty) Ltd.

2.4 Results

2.4.1 *Population structure and growth*

Throughout the course of the study period (March 2016 - May 2017), 180 observations were recorded and a total of 243 individual zebra were indentified from the known 571 individuals counted during the September 2015 aerial survey. The sample used for demographic analyses thus constituted roughly 40% of the known population. The 243 individuals indentified were organised into 32 bands (family groups) and 46 individual bachelor males. The sampled population was comprised of 168 adults (69.1%), 32 yearlings (13.2%) and 43 foals (17.7%) (Table 2.1, Figure 2.2). The sex ratio of adult zebra in MWR was 0.8:1.0 (male:female), but was undeterminable for yearlings and foals (Table 2.1).

Table 2.1 Age and sex structure of the plains zebra population in Majete Wildlife Reserve, Malawi (2016-2017). Sex for 58 foals and yearlings was not determined.

Age Class	Total	Males	Females	Unknown Sex	Sex Ratio	Age Class Proportion of Population (%)
Adults (>24 months)	168	76	92	-	0.8:1.0	69.1
Yearlings (12-24 months)	32	6	8	18	-	13.2
Foals (<12 months)	43	2	1	40	-	17.7
Total	243	84	101	58	-	100.0%

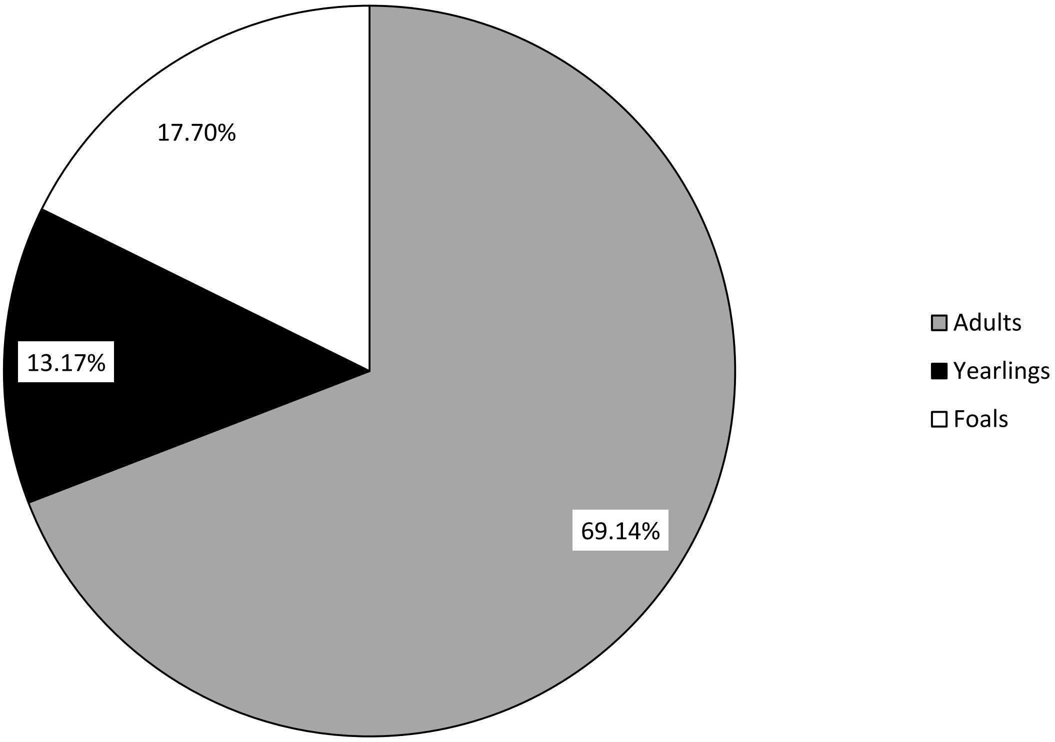

Figure 2.2 The proportional representation of each age class in the plains zebra population in Majete Wildlife Reserve, Malawi for the years 2016 and early 2017

2.4.2 *Bands and bachelor groups*

Within MWR, the band size of zebra varied from two to eleven individuals (mean = 6.3 ± 0.21 [SE]) and each band was comprised of a single adult male with one to five adult females (mean = 2.8 ± 0.10) and their offspring (Table 2.2). The number of yearlings observed within a single band varied from zero to three (mean = 0.6 ± 0.09) and the number of foals varied from zero to four (mean = 1.5 ± 0.11) (Table 2.2). Bachelor males were either observed alone or within groups comprised of two to eight males (mean = 3.0 ± 0.21) (Table 2.2).

Table 2.2 Social structure and size of bands and bachelor groups observed in Majete Wildlife Reserve, Malawi.

BANDS	**Minimum**	**Maximum**	**Mean ± SE**
Adult Males	1	1	1
Adult Females	1	5	2.8 ± 0.10
Yearlings	0	3	0.6 ± 0.09
Foals	0	4	1.5 ± 0.11
Band size	2	11	6.3 ± 0.21
BACHELOR GROUPS	**Minimum**	**Maximum**	**Mean**
Adult Males	1	8	3.0 ± 0.21

Family bands (32 known family bands) that were encountered more than once (n = 59) during the study period retained the exact same adult members (50 encounters), except on nine occasions when members more than two years of age were observed missing from the original family band and sighted occurring with a new band, or when new members more than two years in age joined a well-known group (Figure 2.3). When bachelor males (46 previously identified) were encountered more than once (n = 35), they generally occurred with other bachelor associations (33 encounters), except on two occasions when bachelor bands consisting of two or more adult male members were consistent of the exact same members when re-encounterd (Figure 2.3). The stability of adult members within family and bachelor bands were found to be significantly different (Mann-Whitney U-Test: U = 216.5, Z = -6.38, $p < 0.001$).

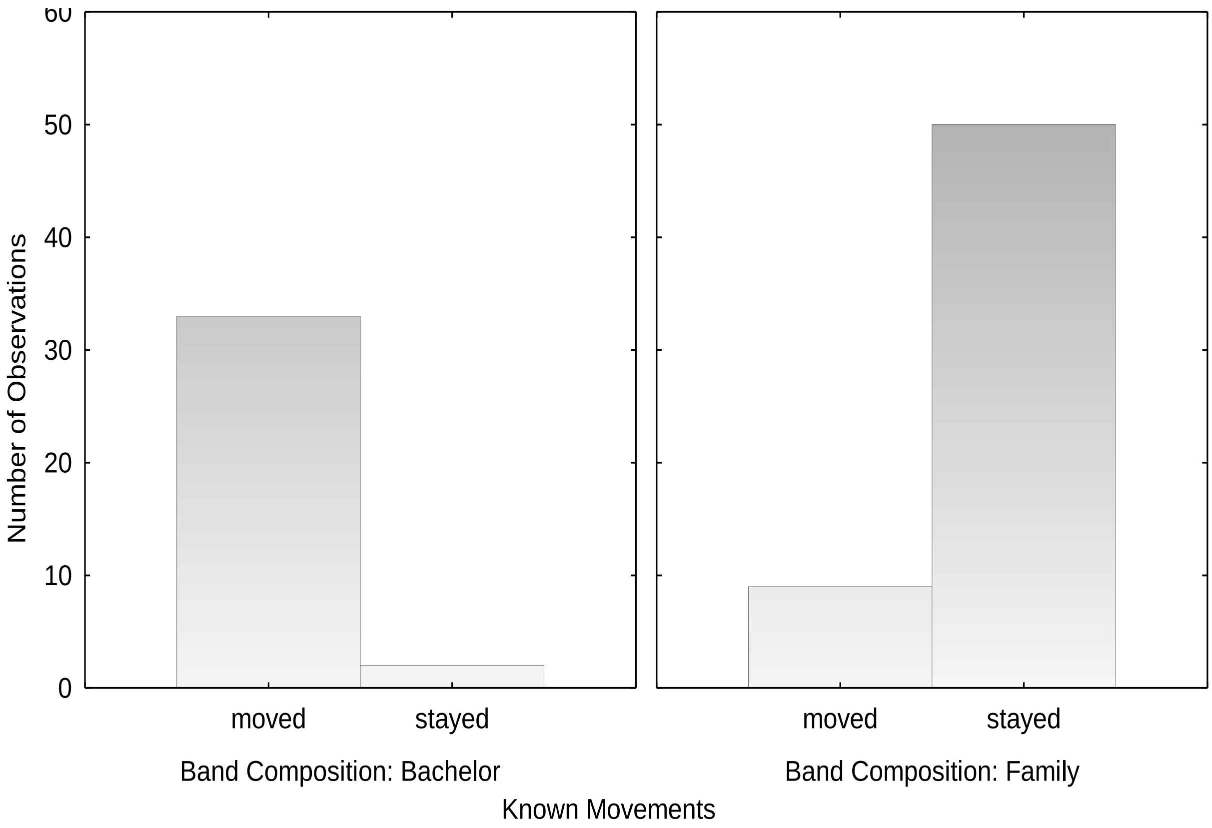

Figure 2.3 Plains zebra band fidelity as shown by the number of observations for which individuals in bachelor bands and family bands changed bands or persisted in their band as compared to their previously observed association.

A positive relationship also occurred between band size and the relative number of foals and yearlings (Figure 2.4) ($p = 0.001$, $r^2 = 0.11$). However, a much weaker and non-significant relationship occurred between band size and only the relative number of foals ($p = 0.16$, $r^2 = 0.02$).

Herds of zebra (multiple bands associating together) were never observed within MWR.

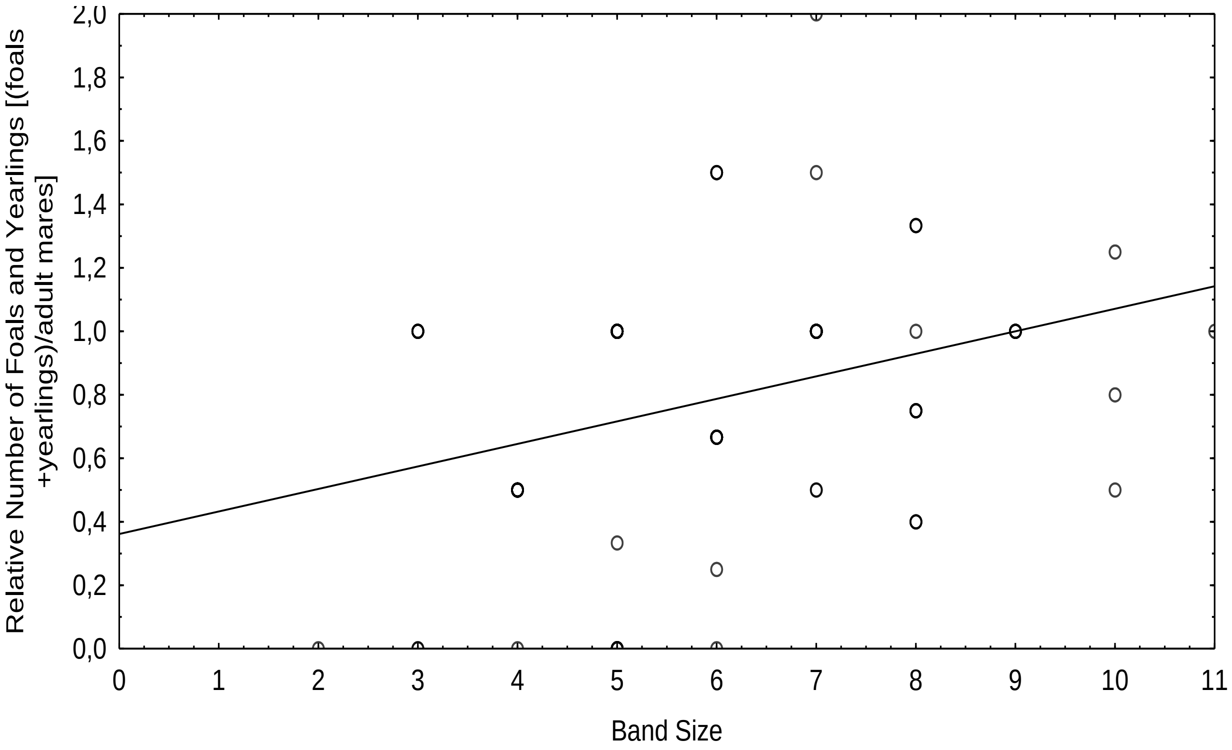

Figure 2.4 The relationship between band size and relative number of foals and yearlings [(foals+yearlings)/adult females] in Majete Wildlife Reserve ($p = 0.001$, $r^2 = 0.11$)

2.4.3 *Distribution*

Zebra locations in Majete Wildlife Reserve as detected from an aerial survey (2015), camera traps and driving transects (March 2016 to March 2017), demonstrate densities decreasing from east to west (Figure 2.5). In the reserve, individual zebra occur at a density of 0.8/km^2 and bands at 0.1/km^2. Driving transects proved to be the least successful method for detecting zebra, especially in the western region of the reserve. Both aerial surveys and camera traps were able to detect zebra successfully throughout the entire reserve.

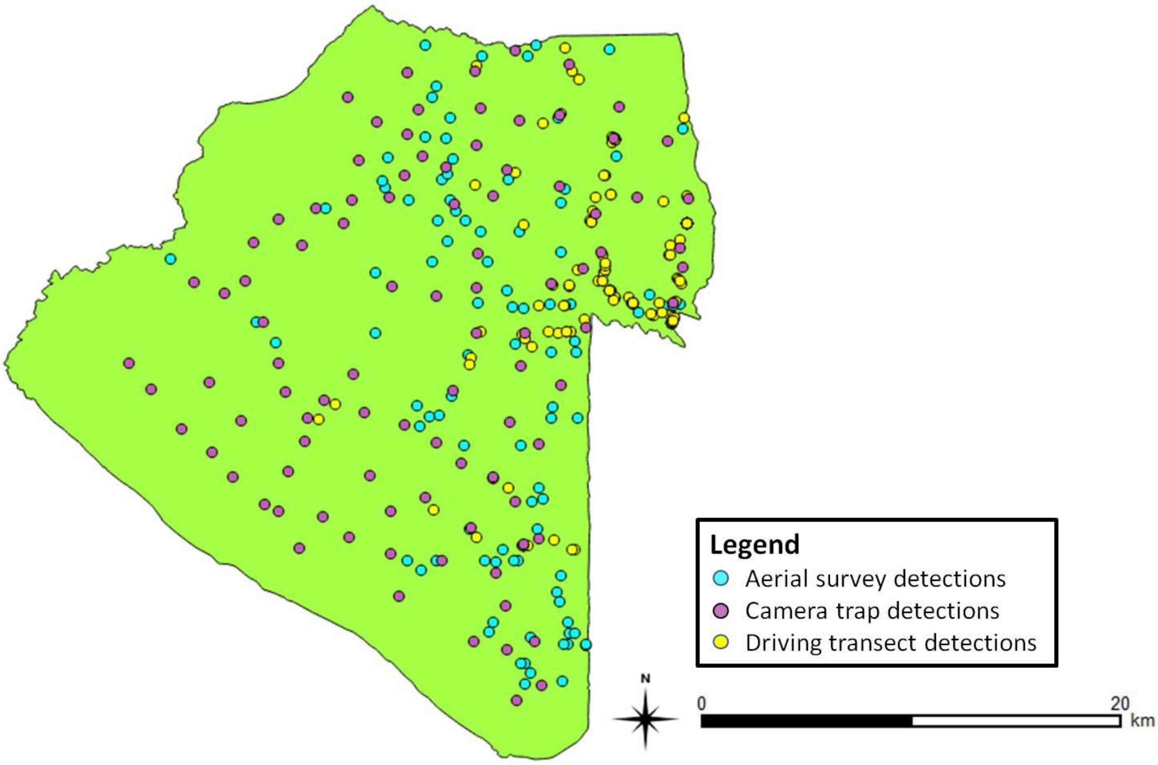

Figure 2.5 A map representing the distribution of plains zebra in Majete Wildlife Reserve, Malawi, as detected from an aerial survey (blue), camera traps (purple) and driving transects (yellow)

2.5 Discussion

Plains zebra have successfully established in MWR after the reintroduction of 174 animals between 2004 and 2009. In general, a population would be expected to exhibit a lag interval after reintroduction, before a period of rapid growth (Chivers, 1991; Saltz & Rubenstein, 1995). The apparent high rate of population growth confirms that the zebra have overcome any initial stress of translocation, that they are successfully establishing within the reserve and that the rapid growth rate had been maintained. Compared to other equid reintroductions, the growth rate of MWR's zebra population appears very high. The high growth rate may have arose from a female biased founder population of a polygynous species or may reflect a lack of environmental pressures, for example predation.

Reintroduced Cape mountain zebra (*Equus zebra zebra*) in South Africa experienced an annual growth rate of 0.4% for the first three to five years after reintroduction compared to a subsequent growth rate of 9.3% for the next three to five years (Kaczensky *et al*., 2016; Novellie, Millar & Lloyd, 1996). In South Africa the highest annual population growth rate for plains zebra after reintroduction was recorded as 23% (Hack *et al*., 2002). Across their range, the mean population growth rate for plains zebra populations at carrying capacity, ranges from only 0.92 - 1.01%, indicating that substantial environmental, anthropogenic and predation pressures typically influence growth in established populations of this species at their current density (Ransom *et al*., 2016). We can thus imply that the zebra in MWR have not yet reached the carrying capacity of the reserve, even though they are approaching it and that environmental, anthropogenic and predator pressures are not limiting their growth.

Plains zebra have dispersed throughout the entire reserve, although densities decreased from east to west. This may be a result of dispersal limitation, as zebra were only reintroduced into the north-eastern area (134 individuals) and the southern section (40 individuals) of the reserve (Wienand, 2013). Another possibility is that zebra prefer to inhabit the eastern and southern region to the western region of MWR, since the western region is at a higher altitude, has less permanent water sources and less favourable vegetation for zebra as it is dominated more by trees and shrubs, than by grasses (Forrer, 2016; Sherry, 1989; Wienand, 2013). However, the western region of the reserve could possibly have been under sampled by the aerial survey and driving transects, due to increased canopy cover, thicker vegetation, fewer roads and the general logistical difficulty of sampling that region of the reserve, although camera traps were successfully able to capture zebra within the western section.

The population structure of MWR’s zebra appears similar to some well-established zebra populations across Africa, though some differences in social organization were detected. The sample population of MWR was comprised of 69.1% adults, 13.2% yearlings and 17.7% foals; in Hwange National Park, Zimbabwe, the population was comprised of 62 - 63% adults, 13% yearlings and 24 - 25% foals and the population in Laikipia, Kenya, comprised of 75% adults, 15% sub-adults (1 - 3.4 years old) and 10% foals (Georgiadis *et al*., 2003; Grange, 2006).

The adult sex ratio of 0.8:1.0 in MWR was similar to Kruger National Park’s ratio of 0.75:1 and Laikipia, Kenya’s ratio of 0.73:1 (Georgiadis *et al*., 2003; Mills & Shenk, 1992). It is also within the range of the lowest (0.56:1 for Ngorongoro Crater, Tanzania) and the highest (1:1 for Nyika National Park, Malawi) adult sex ratio reported by Hack *et al*. (2002). It is possible that in both our study and comparative studies that males are undercounted and thus reported sex ratios are female-biased. This is because small groups, and especially solitary animals, are most likely to be missed during counts (Ransom, 2012).

The band size of zebra in MWR is within the range of established populations elsewhere in Africa (Table 2.3). In MWR, band size ranged from 2 - 11 (mean = 6.3 ± 0.21), which is the same range as reported for Kruger National Park, South Africa (range = 2 - 11, mean = 4.0 - 4.5) (Smuts, 1976), and similar to Akagera National Park, Rwanda (range = 3 - 14, mean = 7.1) (Monfort & Monfort, 1978). The mean band size for MWR is also in agreement with the mean band sizes reported by Hack *et al*. (2002) which ranged between 4.2 for Kruger National Park, South Africa and 8.2 for Samburu National Park, Kenya.

Band size is possibly influenced by a variety of intrinsic and extrinsic factors and a change in the environmental pressures will likely result in a change in group size (Boyd *et al*., 2016; Rubenstein, 1986). For example in cases where predation, grass height and thicket density were much lower, band size tended to be larger (Grubb, 1981; Smuts, 1976). In MWR the vegetation is predominantly miombo savanna woodlands - typically high grass and very thick vegetation, which is generally not as favoured by zebra as low grass height and low thicket density (Forrer, 2016; Sherry, 1989). Therefore, it is assumed that predation has a stronger effect on the mean band size of zebra in MWR, since predators, though present, occur at densities far below the suggested carrying capacity. In MWR, only 8 lions and an estimated 11 leopards and 18 hyenas occur within the reserve instead of a suggested 53 lions, 22 leopards and 94 hyenas (Briers-Louw, 2017). Furthermore, it has been established that lion, leopard and hyena populations in MWR select for plains zebra at a frequency of 2.98%, 0% and 8.29%, respectively; and that zebra only contribute to 4.25% of biomass consumed by lion, 0% of biomass consumed by leopard and 14.04% of biomass consumed by hyena, indicating that predators in MWR do not preferentially target zebra (Briers-Louw, 2017).

It has also been suggested that a strongly female-biased adult sex ratio can result in exceptionally larger band sizes for harem-forming species (Boyd *et al.*, 2016). The formation of larger bands can also be promoted when a population nears its carrying capacity (Lloyd & Rasa, 1989). However, when comparing the results of this study to others, it appears that the maximum band size of zebra may increase from south to north across Africa, but not enough data were presented in all studies to determine if a significant difference exists in mean band size (Table 2.3). This could either be due to current environmental factors such as spatial distribution of vegetation classes or predator densities concurrent with all prey species abundances, or could be attributed to differences in subspecies (i.e. evolutionary scale influences of those same environmental factors). Further studies will be needed to investigate this phenomenon.

Table 2.3 Summary of band size (mean and maximum) for plains zebra populations throughout the species' range (along a south to north continuum).

	Band Size		
Site	**Mean**	**Maximum**	**References**
South Africa			
Kruger National Park	4.0 – 4.5	8 - 11	Gasaway et *al*., 1996; Hack *et al.*, 2002; Klingel, 1969; Smuts, 1976
Zimbabwe			
Hwange National Park	4.6	8	Hack *et al.*, 2002*;* Klingel, 1969
Namibia			
Etosha National Park	4.7	9	Gasaway et *al*., 1996; Hack *et al*., 2002; Klingel, 1969
Malawi			
Majete Wildlife Reserve	6.3	11	
Tanzania			
Rukwa area	5.4	10	Klingel, 1967
Ngorongoro Crater	5.0 – 7.7	10 – 16	Klingel, 1969, 1975
Serengeti National Park	5.1	11	Klingel, 1969; Sinclair & Griffiths, 1982
Rwanda			
Akagera National Park	7.1	14	Monfort & Monfort, 1978
Kenya			
Samburu National Park	8.2	14	Ohsawa, 1982; Rubenstein, 1989;

The general agreement between band and bachelor group data for MWR and the rest of Africa proposes that the social structure of plains zebra at the coarse scale is similar across the species' range, irrespective of environmental pressures (Lloyd & Rasa, 1989). In MWR the bachelor group size ranged from one to eight individuals with a mean of 3.0

± 0.21, compared to the one to seven individuals with a mean of two to three in Kruger National Park, South Africa (Grubb, 1981). Even though the maximum number of individual bachelors aggregating together has been recorded as high as 50 individuals, bachelor groups generally consist of only three males (Hack *et al*., 2002; Linklater, 2000). Furthermore, the mean number of adult females within a band in MWR was estimated to be 2.8 ± 0.10, and corresponds to the mean number of adult females of 2.2 - 2.8 in Kruger National Park, South Africa, Etosha National Park, Namibia, and Hwange National Park, Zimbabwe, as well as Serengeti National Park and Ngorongoro Crater, Tanzania (Hack *et al*., 2002). Of these, Etosha, Hwange and Serengeti National Parks, also had a maximum of five adult females within a band (Gasaway *et al*., 1996; Klingel, 1969). Similar to the findings of this study, a band generally only includes a single adult stallion (Boyd *et al*., 2016; Fischhoff *et al*., 2007; Hack *et al*., 2002; Klingel, 1969; Pluhácek & Bartos, 2005). Unfortunately, no mean or maximum data on the number of foals or yearlings within a band is available for comparison.

A positive significant relationship exists between band size and the relative number of foals and yearlings. This corresponds to other studies conducted on equids (Kaseda & Khalil, 1996; Pacheco & Herrera, 1997). There was no relationship between band size and only foal production in our study, which may indicate that the true benefit to larger bands may be in overall recruitment success rather than fecundity in general. Female zebra therefore benefit from living in larger groups, as this structure has the potential to increase their reproductive success by decreasing their exposure to bachelor harassment and increasing their time spent foraging (Rubenstein, 1994). Larger bands also have the potential advantages of occupying better-quality home ranges and spending less time being vigilant, consequently enhancing their reproductive success (Pacheco & Herrera, 1997; Rubenstein, 2010).

Bands were found to be more stable than bachelor groups; but even though bachelor groups were highly unstable, some bachelor dyads were observed together for several months. This is in agreement with other studies conducted by Klingel (1969, 1975) and Rubenstein (1986) on plains zebra, as well as a study conducted on mountain zebra by Penzhorn (1984). The stable bonds between adult family band members may serve more than one function, however the function of stable bonds between wild adult zebra has not been previously investigated (Simpson *et al*., 2012). It is hypothesized that members can benefit from the shared protection of offspring and reduced aggression over the utilization of shared resources due to stable bonds between family members (Boyd *et al*., 2016; Simpson *et al*., 2012). In contrast, bachelor groups tend to experience higher levels of competition and aggression likely resulting in less stable bonds (King *et al.*, 2016). It is, however, hypothesized that bachelor groups form in order for members to gain protection from predation. Young males can also learn fighting skills and gain the opportunity to attain females jointly (Boyd *et al*., 2016).

The formation of herds (multiple bands associating together) in MWR was never observed. Herds generally form when resources are abundant, bachelor harassments frequent and the risk of predation high (Rubenstein, 2010). Yet, herds has the potential to increase resource competition (Rubenstein, 1994, 2010). The reason why the formation of herds was never observed in MWR could be because 1) resources can become limited in MWR, especially the availability of forage during the dry season due to its severity, extremely high temperatures and lack of water (Bell, 1984; Forrer, 2016); 2) the adult male:female ratio is slightly biased from a 1:1 parity (0.83:1), which may result in lower than normal frequencies of bachelor harassments; and 3) predation pressures are low due to a small predator population in the reserve occurring at very low densities (Briers-Louw, 2017). Thus, the costs of living in herds do not outweigh the benefits in MWR.

2.6 Conclusion

The reintroduction effort for plains zebra at MWR appears to have resulted in successful establishment of a population that generally reflects the social structure and organization found in established populations. The results of this study suggest that plains zebra possess the ability to recover when reintroduced into a suitable habitat and protected from overhunting (King & Moehlman, 2016). The biased sex ratio and lack of herd formation may be an artefact of the founding population structure (which was more female-baised) in concert with environmental factors, for example predation pressures and resource availability. Ultimately, such decisions on which animals form the founding populations must be balanced between management goals, costs, and priorities, and the intended naturalness of the future population. The reintroduction of primarily family bands at MWR appears to have struck that balance within a decade after release, as the population within MWR has successfully established, are displaying high annual growth rates and starting to mimic the sex and age structure of well-established population throughout the rest of Africa. Active management (translocations or establishment of an established predator population) and monitoring (aerial, mark-resight and simultaneous doble-count surveys) is still needed as this population continues to grow towards carrying capacity and with changing resource conditions. Small, fenced reserves also require more active management and monitoring and this will prevent zebra for becoming extirpated again from MWR.

Even though this study has contributed towards our understanding on the demographics of MWR's zebra more than ten years after their initial reintroduction, our understanding of this population can be improved by conducting further research, including:

1) Developing more precise measures of population growth through surveys that employ statistical sampling techniques such as mark-resight, simultaneous double-count, line transect surveys, or techniques that combine these methods to address the wooded conditions of MWR (Laake, Dawson & Hone, 2008; Lubow & Ransom, 2016; Williams, Nichols & Conroy, 2002). Such estimates will in turn allow more robust population modelling and deeper understanding of the dynamics at work for zebra at Majete. By investigating the population growth, management will also be able to determine when the population has reached its carrying capacity or if the population is starting to decline.

2) By continuing this specific study over a longer time frame the annual production rate of foals can also be calculated, as well as their survival rates. The age of dispersal (the age young females or males will leave their natal bands) could then also be investigated, as well as the amount of times an individual zebra will change bands before settling, how long a stallion's tenure will last before a new male abducts its harem and how long stable bonds between family band members will persist.

3) Factors influencing the distribution of zebra throughout the reserve can be determined by integrating ground-truthed vegetation maps (which will be available at the end of 2017, C. Hay & M. Scalbert, personal communication, May 10, 2017) as well as the location of natural and artificial water sources in order to determine if vegetation types

and/or the location of surface water are driving the distribution of MWR's zebra. This can be analysed using ArcGIS 10.5 (Environmental Systems Research Institute, Redlands, California, U.S.A.).

4) Other studies have reported that zebra dynamics appear to be strongly affected by the annual fluctuation in rainfall (Georgiadis *et al.*, 2003). If the population estimates from aerial surveys (of at least 20 years) can be compared with the annual rainfall received for each of those specific years, then it can be determined whether rainfall influences the dynamics of MWR's zebra population.

5) Other studies have also found that zebra populations are limited by predation (Grange *et al.*, 2015). Currently, MWR's predators are limited in number (as previously discussed) and this represents a remarkable opportunity to determine how an increase in predator numbers will affect the zebra population by continuing to investigate both the demographics and population estimates of the reserves zebra, along with a change in the population size of the predators. Mark recapture methods, as well as kill site investigations can provide valuable information on what age or sex predators are selecting for (Grange, 2006; Briers-Louw, 2017). Whereas aerial surveys will be able to provide information on how the population is affected by an increase in predator number.

6) The development of a computer program that can accurately assist with the identification of zebra (even when vegetation particularly obscures some of the stripes) would be highly beneficial. A program like this would not only save a lot of time spent identifying individuals, but will possibly result in a larger proportion of zebra being identified. In addition, it will also assist future researchers with identifying zebra that has previously been identified by this study.

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Chapter Three

Stable isotope analysis of the diet of the plains zebra (*Equus quagga*) in Majete Wildlife Reserve, Malawi

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3.1 Abstract

The abundance and seasonal variation of forage is a key factor determining the habitat use and movement of animals across the world. Plains zebra (*Equus quagga*) typically inhabit grasslands, but they also occur in more wooded environments, such as the historic population in miombo savanna woodlands of Majete Wildlife Reserve (MWR), Malawi, prior to extirpation. From 2004 to 2009, plains zebra were reintroduced to MWR and have since experienced substantial population growth, distributing themselves across the reserve. The extent to which plains zebra can exploit browse in miombo savanna woodland is unknown and ultimately may be a limiting factor for populations in such environments. This study aimed to investigate the plasticity and seasonal change in plains zebra's consumption of C_4 grass and C_3 browse (trees, shrubs and forbs) in MWR with the use of stable isotope analysis of faecal samples. Stable isotope analysis is a method used to determine the contribution of C_3 and C_4 food sources in the diet of animals and is based on our understanding of photosynthesis. We determined that the diet of plains zebra at Majete Wildlife Reserve predominantly consisted of C_4 grasses (84.0 - 100.0%). However, a significant seasonal change did occur with the proportion of C_4 grasses decreasing from 98.6% during the late wet season to 92.8% during the early dry season and 89.8% during the late dry season (Kruskal-Wallis test: $H = 29.47$, $p < 0.001$). Conversely, the contribution of C_3 browse to the diet of plains zebra increased as the C_4

grasses decreased. Plains zebra in this study exhibited limited dietary plasticity, even when inhabiting the browse-rich environment of MWR's miombo savanna woodland ecosystem. The zebra in Majete did occasionally browse to sustain protein levels due to a lack in quality and quantity of graze available, especially during the late dry season, but the evolution of a diet consistent of more browse may ultimately be limited by presence of C_4 grasses within the reserve.

3.2 Introduction

Plains zebra (*Equus quagga*) are typically pure grazers (Bodenstein, Meissner & van Hoven, 2000; Dekker, 1997; Owaga, 1975; Rubenstein, Cao & Chi, 2016). They occur in open savannas, where grasses are abundant, or in open woodlands and their migration routes follow the abundance of grasses across seasons (Bell 1971; Schoenecker, King, Nordquist, Nandintsetseg & Cao, 2016; Young, Palmer & Gadd, 2005). When investigating their movement at a larger scale, plains zebra were found to track the long grasses that sprout after the rains (Bell 1971; Young *et al*., 2005). At a finer scale, their movement is influenced by the cost and benefits of maximizing their food intake while minimizing their predation risk. Thus, plains zebras optimize their nutritional intake by migrating to prime grasslands, where they can select for higher-quality food resources rather than low-quality abundant forage. However, not all plains zebra populations migrate (Schoenecker *et al*., 2016).

Studies conducted on the dietary preference of non-migratory plains zebras have indicated that the species tend to graze on C_4 grasses (Owaga, 1975; Rubenstein *et al*., 2016). This is confirmed by a study conducted in Kruger National Park, South Africa, which estimated that the plains zebra's diet consists of 95% C_4 grasses and that there is little variation in the percentage of C_4 intake between the different seasons (Codron *et al*., 2005). This can be due to the fact that plains zebra, unlike ruminants, have a specialized digestive system that enables them to consume large quantities of low-quality vegetation (Schoenecker *et al*., 2016). This allows plains zebra to select areas with the highest biomass of grasses regardless of quality, and results in reduced competition with other herbivores, especially during the dry season (Brooks, 2005; Groom & Harris, 2009; McNaughton, 1985).

In Etosha National Park, Namibia, and Hluhluwe-iMfolozi Park, South Africa, plains zebra shifted their diet in the wet season to include higher quantities of short-grass species and in the dry season to include higher quantities of long-grass species (Arsenault & Owen-Smith, 2011; Havarua, Turner & Mfune, 2014). This corresponds with the findings of a study conducted on plains zebra in the Athi-Kaputei plains in Kenya which also observed the dietary shift from short-grass species in the wet season to long-grass species in the dry season (Owaga, 1975). Arsenault and Owen-Smith (2011) suggested that this dietary shift of consuming larger quantities of poorer quality grasses during the dry season may be as a result of the plains zebra's survival strategy - to enable them to obtain the necessary nutrient requirements by foraging on more readily available foliage of poorer quality rather than sparsely available foliage of higher quality. This observed seasonal change in the abundance and quality of vegetation availability to grazers is shaped by the seasonal variation in precipitation and temperature (Rubenstein *et al*., 2016). However, it has also been documented that plains zebra do occasionally browse to sustain sufficient protein levels and even eat dry leaves during the dry season (Berry & Louw, 1982; McNaughton, 1985). Yet, the extent of browsing is small; for example studies conducted on plains zebra in South Africa have observed that the mean annual intake of grasses is 81.92%, with forbs at 7.0% and browse at only 1.5% (Arsenault & Owen-Smith, 2011; Landman & Kerley, 2001).

One of the methods that has been used for several decades to determine the relative contribution of C_3 and C_4 food sources for diet analysis is stable isotope analysis (Schoenecker *et al*., 2016). This technique is based on our understanding of photosynthesis in plants, since C_3 photosynthesising plants can generally be referred to as browse (trees, shrubs and forbs) and C_4 as grass (monocotyledonous grasses) (Ambrose & Deniro, 1986; Cerling, Harris & Passey, 2003; Deniro & Epstein, 1978; Hobson, 1999; Hofmann & Stewart, 1972; Phillips, 2001; Phillips & Gregg, 2001; Tiezen, Boutton, Tesdahl & Slade, 1983). Upon consumption, the isotope compositions of plants are passed onto animals, with some fractionation (Cerling & Harris, 1999). Therefore browsers have much lower tissue ^{13}C:^{12}C ratios than do grazers since the consumer's tissues and excreta reflect the carbon from their food (Sponheimer *et al*., 2003a).

The carbon and nitrogen isotope composition of an animal's diet can be reflected in hair, teeth, muscle, blood or faecal matter and detected with the use of a mass spectrometer (Deniro & Epstein, 1978; Sandberg, Loudon & Sponheiner, 2012; Schoenecker *et al*., 2016; Sponheimer *et al*., 2003b). Long-lived tissues can reveal dietary variation over months or years, and faeces over a few days, thus stable isotope analyses can allow for the study of a species diet at different time scales (Cerling *et al.* 2003; Codron *et al.* 2005; Codron *et al.* 2007). A mathematic correction is needed when analysing long-lived tissue, as the growth rate and attenuation time is significantly higher than in faecal matter (Codron *et al.* 2007). The collection of faecal matter in the field is easier, less invasive and less stressful towards the study animals than the sampling of hair, teeth, muscle or blood (Codron *et al.* 2005; Codron *et al.* 2007). Even though faeces display the proportion of C_3 and C_4 food sources in an individual's diet, it is important to note that faecal matter is only a partial reflection of the true diet of an individual as it only contains the undigested portion of the diet (Codron *et al.* 2005; Codron *et al.* 2007). Testing the variation in the contribution of grass and browse to an animal's diet with the use of carbon isotope analysis can prove challenging as the differences in the faecal $\delta^{13}C$ are generally minute. In addition, the differences in the faecal $\delta^{13}C$ may also be due to a variation in NAD-ME/PCK and NAD-ME type grasses (Cerling & Harris, 1999).

Isotope values of tissue or faecal samples can be compared to the isotope values obtained from forage samples using an analysis program (IsoSource) (Schoenecker *et al*., 2016). The $\delta^{13}C$ values of tropic and subtropic trees and shrubs generally range between -22 and -35‰ and the $\delta^{13}C$ values of tropical grasses between -10 and -15‰ (Cerling, Harris & Leakey, 1999). Ranges that illustrate all possible source contributions to the tissue or faecal sample are given by IsoSource (Nordquist, 2011). However, according to Schoenecker *et al*. (2016): "IsoSource is limited in the number of sources that can be put into the program."

While plains zebra typically inhabit grasslands, they also occur in more wooded environments, such as the historic population in miombo woodlands of Majete Wildlife Reserve (MWR), Malawi, prior to extirpation. From 2004 to 2009, plains zebra were reintroduced to MWR and have since experienced substantial population growth, distributing themselves across the reserve (see Chapter 2). The extent to which zebra can exploit browse in miombo woodland is unknown and ultimately may be a limiting factor for populations in such environments. The aim of this study was to determine the seasonal dietary composition and the extent of dietary plasticity of plains zebra in MWR, using stable isotope analysis of their faecal matter. The hypothesis for this study was that the diet of plains zebra would predominantly consist of grass with the occasional utilization of browse, despite the more limited availability of grasses and predominance of browse. It was also hypothesised that plains zebra in MWR would utilize more browse than plains zebra living in pure savanna habitat. The abundance and type of forage consumed is the best predictor of equine habitat use and movement (Schoenecker *et al.*, 2016; Smuts, 1975; Williams, 1998). Since it is important to develop and execute suitable conservation management actions based on the extent of dietary flexibility of animals, the results and knowledge gained from this study will be taken into consideration when offering conservation recommendations to the management team of MWR (Radloff, van der Waal & Bond, 2013).

3.3 Methods

3.3.1 Study site

MWR covers 700km^2 and is situated in southern Malawi, in the Lower Shire Valley region. The expected annual rainfall ranges between 680 – 1000mm and the daily temperature averages at 28.4°C in the summer (December – February) and 23.3°C in the winter (June – August) (Gyöngyi, 2011; Spies, 2015; Wienand, 2013). The wet season occurs from December until May (early wet: December – February; late wet: March – May) and the dry season from June to November (early dry: June – August; late dry: September – November).

The altitude increases from east to west – where rolling hills can be found. Two main rivers, namely the Shire River and the Mkulumadzi River, runs through the reserve along with a number of small seasonal rivers (Sherry, 1989; Wienand, 2013). A few perennial springs, temporal pools and ten artificial waterholes are also located within MWR (Wienand, 2013). It is important to note that artificial water points alleviate water availability and extend the forage area available to herbivores during the dry season, thus assisting population growth (Chamaillé-Jammes, Fritz & Murindagomo, 2007; Redfern, Grant, Biggs & Getz, 2003; Wienand, 2013). The vegetation for the most part is miombo savanna woodland. Miombo savanna woodland is a woody savanna formation generally dominated by trees in the genera *Brachystegia*, *Julbernardia* and *Isoberlinia*, as well as an underlying layer of grass (Mwase, Bjørnstad, Bokosi, Kwapata & Stedje, 2007). In MWR, four distinct classes can be identified within the miombo savanna woodland: low altitude (<250m) mixed woodland, medium altitude (250 - 400m) mixed woodland, high altitude (<400m) miombo woodland and savanna (Forrer, 2016; Sherry, 1989). *Acacia* species and *Steculia* are the dominant species found within the low altitude mixed woodland, *Brachystegia boehmii, Diiospyrus kirkii* and *Combretum* species of the medium altitude mixed woodland, *Brachystegia boehmii, Burkea africana* and *Pterocarpus* of the high altitude mixed woodland and *Combretum* species*, Acacia* species and *Panicum* species of the savanna (Forrer, 2016). The soil type is mainly lithosols, including either shallow, stony, ferruginous soils or sandy and loamy soils (Sherry, 1989).

MWR was gazetted a non-hunting area in 1951 and in 1955 proclaimed a game reserve, but by the mid-1990s MWR was almost completely decimated of large game due to a lack of management and high levels of poaching (Gyöngyi, 2011; Sherry, 1989). A public-private partnership (PPP) was established in 2003 between African Park Majete (Pty) Ltd. and the Department of National Parks and Wildlife (DNPW), Malawi in which they aimed to restore Majete – since then Majete became fenced and over 2550 animals from 14 different mammal species have been reintroduced (Wienand, 2013). The current estimate of the total number of animals within Majete is over 13 000 (C. Hay, personal communication, January 26, 2016).

3.3.2 Faecal sampling and stable isotope analysis

Fresh (recently dropped or still wet) plains zebra faecal samples, together with selected vegetation samples, were collected, and dried between 1 April 2016 and 30 April 2017. To guarantee that faecal samples were not contaminated by insects, fungi or soil and that they represented the appropriate season, only fresh samples were collected (Wrench, Meissner, Grant & Casey, 1996). Faecal samples (at least three kidney-shaped dung balls) were collected from the centre of a dung pile. It was assumed that each separate dung pile encountered represented a separate individual. For vegetation samples, different parts (for example leaves, stems, flowers and seeds) of a plant zebra were observed feeding on were collected. Both faecal and vegetation samples were stored in brown paper bags, marked with an identity number, date and GPS location. Once faecal samples were collected, samples were left in the sun to dry thoroughly, whereas vegetation samples were preserved in a plant press.

Eight vegetation samples were selected to contribute to the results from previous stable isotope studies conducted in MWR. Of the 63 faecal samples collected, 49 were selected for stable isotope analysis (the rest were discarded due to mould or if they were collected during the early wet season) so that the C_3 and C_4 ratios could be compared between the different seasons. The early wet season (December 2016 – February 2017) was excluded from the analysis as not enough samples were collected for a reliable comparison. The distinct seasons were categorized as: late wet season (April – May 2016 and March – April 2017), early dry season (June – August 2016) and late dry season (September – November 2016).

Faecal and vegetation samples were prepared by the first author and analysed at the Stable Isotope Laboratory of the Mammal Research Institute at the University of Pretoria from 7 – 11 August 2017. Samples were prepared by oven drying them at 60°C for 24 hours. Faecal samples were then mill-grind by hand using a pestle and a mortar. A Beadbug Microtube Homogeniser 115V (USA), running at 330rmp for 6 minutes, was used to mill-grind the vegetation samples into a fine powder. Both faecal and vegetation samples had to be powder fine in order to pass through a 1mm sieve. Aliquots of 1.0 – 1.2mg (faecal/vegetation samples) were weighed into tin capsules (pre-cleaned with toluene). An automated elemental analyser (Flash EA 1112 Series) combusted each weighted sample separately and then a continuous flow-through inlet system (ConFlo IV) transferred the CO_2 gas produced to the Delta V Plus stable light isotope ratio mass spectrometer (all equipment supplied by Thermo Fischer, Bremen, Germany). After every 5th faecal sample and every 2nd vegetation sample a duplicate sample was run; and after every 11 unknown samples (faecal/vegetation) a laboratory running standard (Merck Gel: $\delta^{13}C$ = -20.57‰, $\delta^{15}N$ = 6.8‰, C% = 43.83, N% = 14.64; DL-Valine: $\delta^{13}C$ = -10.57‰, $\delta^{15}N$ = -6.15‰, C% = 55.50, N% = 11.86) and blank sample were run. These running standards were calibrated against international standards.

3.3.3 *Statistical analysis*

For $\delta^{13}C$ and $\delta^{15}N$ the analytical precision was <0.05‰ and <0.12‰. Data corrections were applied using the values obtained from the Merck Gel during each run; and the values from the DL-Valine standard provided the standard deviation values for the Merck Gel. The C^{13}/C^{12} ratios were expressed according to Cowley *et al*. (2010) and Radloff *et al*. (2013) in which the isotopic ratios (R) are expressed as the delta (δ) notation relative to the Vienna Pee Dee Belemnite (VPDB) standard, as indicated in the equation below (where X = ^{15}N or ^{13}C and R = $^{15}N/^{14}N$ or $^{13}C/^{12}C$):

$$\delta X(‰) = [(R_{sample}-R_{standard})/R_{standard}-1]x1000$$

In the case of duplicates, the average of the two sets of values was used for further analysis.

The average $\delta^{13}C$ values of the most widespread C_4 (grasses) and C_3 (browse) species for Majete was obtained by combining the results of the vegetation samples with results from Forrer (2016) and Spies (2015). The average values were then used to act as endpoint values. Thus the average $\delta^{13}C$ values for C_3 and C_4 plants used was -29.11‰ and -12.86‰. To calculate the proportional contribution of C_4 grass to the diet of zebra in MWR, the following dual-mixing model was used (Codron *et al*., 2005):

$$\%\ C4\ grass\ in\ diet = \frac{(\delta 13CC3\ plants + \Delta\delta 13C - \delta 13Cdung)}{(\delta 13CC3\ plants - \delta 13CC4\ plants)} \times 100$$

where Δδ13C represented the significance of discrimination between vegetation and product (dung). According to Codron *et al*. (2005), Codron and Codron (2009), and Sponheimer *et al*. (2003a), a value of -0.9‰ is accepted for faeces.

Statistica version 13.2 (Dell Software, 2016) was used to conduct both t-tests and ANOVA's. Two tailed t-tests were conducted in order to determine if there was a significant difference between the $\delta^{13}C$ and $\delta^{15}N$ values of C_3 and C_4 plants. A one-way analysis of variance (ANOVA) was conducted to determine if there was a significant difference ($\alpha = 0.05$) in zebra dung $\delta^{13}C$ values between the different seasons; as well as if there was a significant difference in the proportion of browse consumed between the different seasons. Lastly, all isotope values were estimated as mean ± SD.

When evaluating the C_4 contributions to animals' diets, a 15% error in isotope-based derivations are taken into consideration (Sponheimer *et al*., 2003b). However, since this study made use of local vegetation samples and regional data over a relatively small time period, the accuracy of isotope mixing models was enhanced (Post, 2002; Codron *et al*., 2005). Therefore a 10% error in isotope-based derivations of the C_4 contributions to diet, as reported in Condron *et al*. (2007), was used.

3.4 Results

The standard corrected values of $\delta^{13}C$ for the 27 C_4 samples ranged between -11.47‰ and -14.44‰ (mean = -12.86‰ ± 0.85) and the 34 C_3 samples between -26.45‰ and -31.54‰ (mean = -29.11‰ ± 1.26) (Table 3.1). A significant difference occurred between the $\delta^{13}C$ values of the C_3 samples when compared to the C_4 samples (Mann-Whitney U test: Z-value = -6.66, $p < 0.001$). The standard corrected values of $\delta^{15}N$ for the 27 C_4 samples ranged between -3.16‰ and 7.72‰ (mean = 0.60‰ ± 2.40) and the 34 C_3 samples between -3.55‰ and 3.86‰ (mean = 0.03‰ ± 1.88). No significant difference was detected between the $\delta^{15}N$ values of the C_3 samples when compared to the C_4 samples (Mann-Whitney U test: Z-value = -0.62, $p = 0.53$).

Table 3.1 δ^{13}C and δ^{15}N values (‰) of C4 grass and C3 browse specimens used as a reference in the stable isotope analysis of the diet of plains zebra in Majete Wildlife Reserve, Malawi. The standard corrected values were applied using the values obtained from the Merck Gel during each run. The vegetation samples were supplemented with the vegetation samples from Forrer (2016) and Spies (2015).

Species	**Type**	**δ15N**	**δ15N (Std corrected)**	**δ13C**	**δ13C (Std corrected)**	**C:N Ratio**
C4 species						
Chloris virgata	Grass	-2.05	-0.43	-12.11	-13.02	59.87
Cynodon dactylon	Grass	3.16	3.58	-14.32	-14.27	18.33
Cynodon dactylon	Grass	2.30	2.73	-13.85	-13.80	16.85
Cynodon dactylon	Grass	2.49	2.92	-14.50	-14.44	24.78
Dactylotenium aegyptium	Grass	-0.85	0.46	-11.94	-12.84	39.08
Dactylotenium aegyptium	Grass	1.66	2.10	-13.72	-13.68	24.24
Dactylotenium aegyptium	Grass	7.34	7.72	-12.87	-12.85	17.31
Dactylotenium aegyptium	Grass	5.37	5.77	-13.12	-13.09	26.53
Digitaria eriantha	Grass	-2.33	-0.69	-11.07	-11.97	68.86
Erogrotis aspera	Grass	-0.86	-0.90	-15.12	-13.93	45.04
Eragrotis cilianensis	Grass	-3.51	-3.16	-12.70	-13.62	37.29
Heteropogon contortus	Grass	-1.55	-1.60	-14.73	-13.55	43.18
Heteropogon contortus	Grass	-178	-1.83	-14.60	-13.44	47.78
Heteropogon contortus	Grass	-1.26	-0.80	-12.17	-12.17	21.75
Heteropogon contortus	Grass	0.86	1.30	-11.70	-11.72	25.31
Heteropogon contortus	Grass	-0.85	-0.39	-11.56	-11.58	32.75
Hyparrhenia rufa	Grass	-1.97	-1.50	-11.60	-11.62	34.01
Hyparrhenia rufa	Grass	-3.01	-2.53	-11.93	-11.94	40.68
Hyparrhenia rufa	Grass	-2.40	-1.93	-11.45	-11.47	29.09
Panicum maximum	Grass	-0.52	0.60	-11.61	-12.53	31.88
Panicum maximum	Grass	-0.83	-0.88	-14.79	-13.62	45.22
Urochloa mosambicensis	Grass	-0.36	0.36	-11.28	-12.17	20.52
Urochloa mosambicensis	Grass	-0.44	0.69	-11.80	-12.69	28.52
Urochloa mosambicensis	Grass	0.01	1.04	-12.09	-12.99	26.11
Urochloa mosambicensis	Grass	1.15	1.10	-14.42	-13.23	39.85
Urochloa mosambicensis	Grass	0.82	1.27	-12.48	-12.47	19.77
Urochloa mosambicensis	Grass	0.73	1.17	-12.57	-12.56	16.25

C3 species						
Acacia nigrescens	Tree	1.41	1.36	-30.06	-28.90	22.41
Acacia nigrescens	Tree	3.26	3.68	-30.68	-30.20	11.85
Acacia nigrescens	Tree	2.51	2.94	-30.00	-29.54	15.98
Acacia nigrescens	Tree	3.44	3.86	-32.06	-31.54	18.06
Acacia nilotica	Tree	-1.27	-1.15	-31.63	-30.45	30.18
Astystasia gangetica	Forb	2.25	2.50	-30.07	-28.88	16.82
Becium grandiflorum	Shrub	0.24	0.19	-30.95	-29.79	22.08
Brachystegia utilis	Tree	-0.17	-0.22	-27.63	-26.45	35.00
Combretum adenogonium	Tree	-3.15	-3.55	-29.54	-28.36	35.18
Combretum zeyheri	Tree	0.23	0.35	-31.03	-29.85	23.16
Dalbergia melanoxylon	Tree	-0.35	0.10	-29.19	-28.75	12.61
Dalbergia melanoxylon	Tree	-0.64	-0.18	-30.35	-29.78	12.38
Dalbergia melanoxylon	Tree	0.03	0.48	-31.00	-30.51	14.12
Diospyros kirkii	Tree	-2.92	-2.96	-30.15	-28.97	36.49
Diospyros kirkii	Tree	-2.92	-3.03	-30.16	-29.02	37.15
Diplorhynchus condylocarpon	Shrub/Tree	-0.17	-0.22	-29.95	-28.78	26.64
Diplorhynchus condylocarpon	Shrub/Tree	-1.28	-1.33	-29.49	-28.34	29.38
Diplorhynchus condylocarpon	Shrub/Tree	0.61	1.06	-28.13	-27.72	21.84
Diplorhynchus condylocarpon	Shrub/Tree	2.37	2.80	-27.10	-26.72	16.76
Diplorhynchus condylocarpon	Shrub/Tree	1.24	1.68	-27.47	-27.08	19.45
Grewica bicolour	Shrub/Tree	0.44	0.39	-30.71	-29.54	22.33
Julbernardia globiflora	Tree	0.47	0.81	-28.76	-27.60	25.59
Julbernardia globiflora	Tree	0.86	0.42	-28.61	-27.47	26.02
Monotes africanus	Tree	-0.37	-0.24	-30.79	-29.61	29.78
Neorautanenia mitis	Forb	-1.90	-1.95	-30.63	-29.47	14.35
Petrocarpus lucens	Shrub	-0.81	-0.86	-30.11	-28.97	18.01
Petrocarpus lucens	Shrub	-0.82	-0.69	-30.25	-29.07	18.42
Pilea tetraphylla	Forb	0.09	0.04	-32.70	-31.51	14.42
Pseudolachnostylis maprouneifolia	Tree	-3.09	-3.13	-30.05	-28.90	30.89
Pseudolachnostylis maprouneifolia	Tree	-0.37	-0.42	-29.17	-27.97	26.04
Sterculia quinqueloba	Tree	2.23	2.18	-30.92	-29.74	31.16
Tamarindus indica	Tree	-1.04	-1.24	-32.14	-30.65	22.38
Tamarindus indica	Tree	-1.19	-1.08	-31.80	-30.98	20.99
Terminalia sericea	Tree	-1.41	-1.46	-29.80	-28.63	38.38

The corrected $\delta^{15}N$ values of the plains zebra faecal samples ranged between -0.55‰ and 2.92‰ over the sampling period with a mean of 0.95‰ (± 0.88) during the late wet, early dry and late dry seasons (Table 3.2). In addition, the corrected $\delta^{13}C$ values of plains zebra faeces ranged between -13.01‰ and -16.36‰ (mean = -14.72‰ ± 0.87) (Table 3.2). When investigating at a seasonal level, the $\delta^{13}C$ values ranged between -13.01‰ and -14.44‰ (mean = -13.86‰ ± 0.45) during the late wet season, between -14.09‰ and -16.04‰ (mean = -14.94‰ ± 0.54) during the early dry season and between -14.22‰ and -16.36‰ (mean = -15.42‰ ± 0.71) during the late dry season. A significant difference was observed in the $\delta^{13}C$ values of the different seasons (ANOVA: $F_{2,46} = 31.84$, $p < 0.001$). We determined that the $\delta^{13}C$ values of the late wet season were significantly different from both the early dry ($p < 0.001$) and late dry season ($p < 0.001$), but no significant difference was found between the early dry and late dry season ($p = 0.06$).

Table 3.2 $\delta^{13}C$ and $\delta^{15}N$ values (‰) of plains zebra (*Equus quagga*) faecal samples representing their diet during the late wet season (March to May), early dry season (June to August) and late dry season (September to November) in Majete Wildlife Reserve, Malawi. The standard corrected values were applied using the values obtained from the Merck Gel during each run.

Season	δ15 N	δ15N (Std corrected)	δ13 C	δ13C (Std corrected)	C:N Ratio
Late Wet	0.07	2.35	-12.95	-13.65	42.25
Late Wet	-0.93	1.29	-13.10	-13.80	49.86
Late Wet	-0.92	1.03	-13.26	-13.96	46.18
Late Wet	-0.48	2.27	-12.84	-13.54	62.23
Late Wet	-0.42	2.51	-13.03	-13.74	58.23
Late Wet	-1.83	0.74	-13.22	-13.94	49.49
Late Wet	-1.59	0.75	-13.19	-13.92	71.47
Late Wet	-1.63	0.76	-13.62	-14.34	75.46
Late Wet	-0.06	2.53	-13.47	-14.20	45.88
Late Wet	-0.69	2.26	-13.71	-14.44	65.48
Late Wet	-1.71	1.06	-13.54	-14.27	81.27
Late Wet	-1.27	1.75	-13.15	-13.89	80.50
Late Wet	-2.46	-0.09	-13.70	-14.44	89.13
Late Wet	-1.55	1.23	-13.43	-14.18	80.26
Late Wet	-0.52	1.83	-12.28	-13.16	48.79
Late Wet	-0.76	1.75	-12.13	-13.01	53.83
Late Wet	-1.15	1.17	-12.27	-13.15	53.59
Early Dry	-0.80	1.74	-13.55	-14.31	58.75
Early Dry	-0.96	1.47	-13.75	-14.52	61.71
Early Dry	-1.05	2.08	-13.65	-14.41	80.98

Early Dry	-2.03	1.16	-13.32	-14.09	109.09
Early Dry	-1.80	0.79	-14.09	-14.86	73.75
Early Dry	-1.87	0.48	-14.80	-15.58	76.35
Early Dry	-1.61	0.53	-15.26	-16.04	70.67
Early Dry	-2.73	0.33	-14.05	-14.83	70.60
Early Dry	-1.64	1.61	-13.81	-14.60	81.28
Early Dry	-1.50	1.49	-14.97	-15.77	81.25
Early Dry	-1.69	1.14	-13.94	-14.74	84.22
Early Dry	-1.44	0.39	-13.88	-14.68	53.90
Early Dry	-0.54	2.14	-14.31	-15.12	55.27
Early Dry	-0.13	2.92	-14.32	-15.13	65.11
Early Dry	-1.90	0.37	-14.62	-15.44	79.41
Early Dry	-2.45	-0.42	-14.04	-14.86	89.51
Late Dry	-1,94	-0,32	-13,57	-14,25	60,37
Late Dry	-1,78	0,55	-14,25	-14,93	73,69
Late Dry	-2,22	-0,07	-14,40	-15,09	71,85
Late Dry	-1,93	0,32	-13,71	-14,40	74,93
Late Dry	-1,88	0,00	-14,51	-14,22	77,04
Late Dry	-1.99	0,63	-14,28	-15,10	77,20
Late Dry	-2,23	0,08	-14,41	-15,24	84,11
Late Dry	-1,72	0,66	-15,19	-16,03	78,40
Late Dry	-1,92	0,04	-15,11	-15,96	65,89
Late Dry	-1.80	0.61	-14.88	-15.72	74.15
Late Dry	-2,31	-0,55	-15,51	-16,36	72,21
Late Dry	-1,18	0,80	-15,23	-16,08	66,15
Late Dry	-1,79	0,31	-14,90	-15,75	72,30
Late Dry	-2,32	-0,44	-15,16	-16,02	71,36
Late Dry	-2.27	-0.19	-14.42	-15.28	77.32
Late Dry	-2.08	0.79	-15.39	-16.26	86.86

Plains zebra faecal samples contained $\delta^{15}N$ and $\delta^{13}C$ values during the late wet, early dry and late dry seasons, as well as the $\delta^{15}N$ and $\delta^{13}C$ values of C_3 and C_4 vegetation (Figure 3.1). Throughout the entire sampling period, C_4 grasses were the predominant vegetation in the diet of plains zebra and ranged from 84.0% to 100.0% for all faecal samples analysed (Table 3.3).

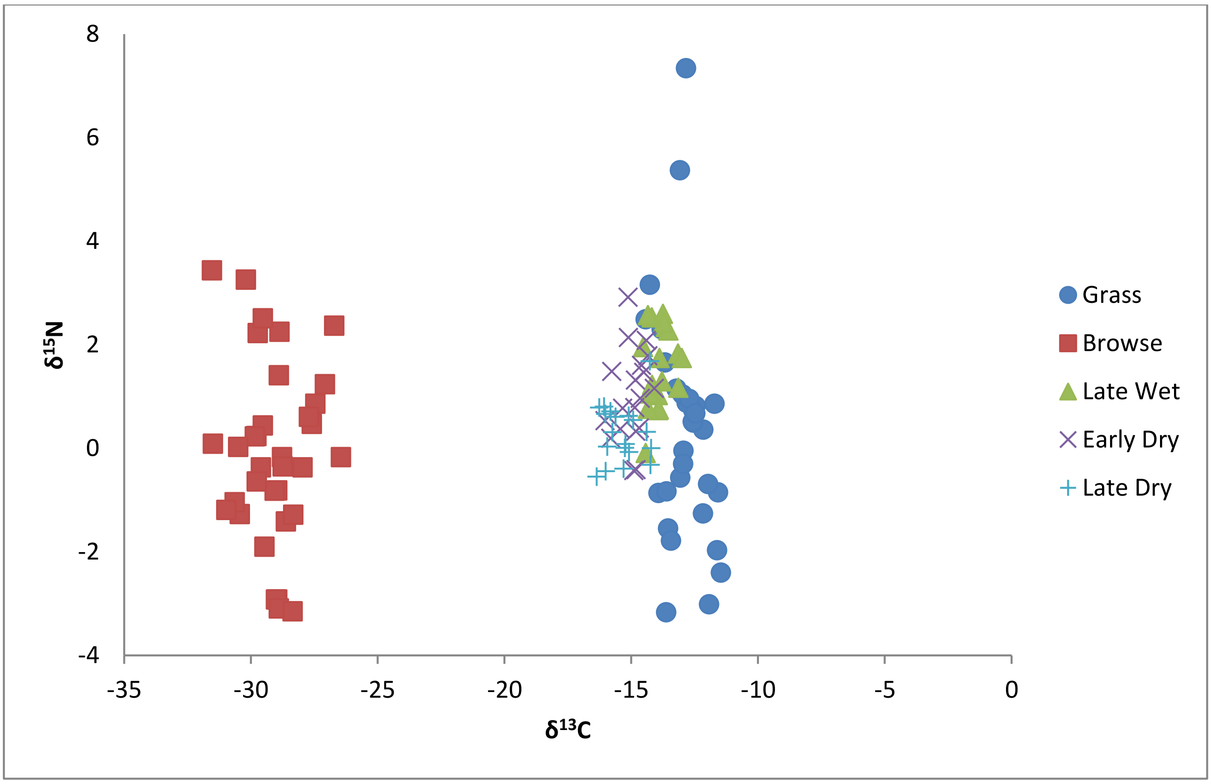

Figure 3.1 The isotope values of C_4 and C_3 vegetation samples, along with the isotope values of carbon and nitrogen in the diet of plains zebra (E*quus quagga*) in the late wet season, early dry season and late dry season in Majete Wildlife Reserve, Malawi

Table 3.3 Mean percentage grass and browse consumption, as well as the range indicated in parentheses, for plains zebra (E*quus quagga*) during the late wet season, early dry season and late dry season in Majete Wildlife Reserve, Malawi.

Season	**N**	**Zebra δ13C (‰)**	**±SD**	**Zebra % grass (range)**	**Zebra % browse (range)**
Late Wet	17	-13.86	0.45	98.6 (95.8 - 100.0)	1.5 (0.0 - 4.2)
Early Dry	16	-14.94	0.54	92.8 (86.0 – 98.0)	7.2 (2.0 - 14.0)
Late Dry	16	-15.42	0.71	89.8 (84.0 - 97.2)	10.2 (2.8 - 16.0)

However, the proportion of C_4 grass consumed decreased slightly as the season's progressed from late wet to late dry (Figure 3.2; Table 3.3). Conversely, the proportion of C_3 vegetation increased from 1.5% during the late wet season to 7.2% during the early dry season and to 10.2% during the late dry season (Figure 3.2; Table 3.3). In addition, a Kruskal-Wallis test confirmed a significant difference in the proportion of browse consumed between the different seasons ($H = 29.47$, $p < 0.001$). On a finer scale, the proportion of browse consumed during the late wet season (mean = 1.5 ± 1.59) was significantly different from the early dry (mean = 7.2 ± 3.35) and late dry season (mean = 10.2 ± 4.39), but no significant difference was detected between the early dry and late dry season.

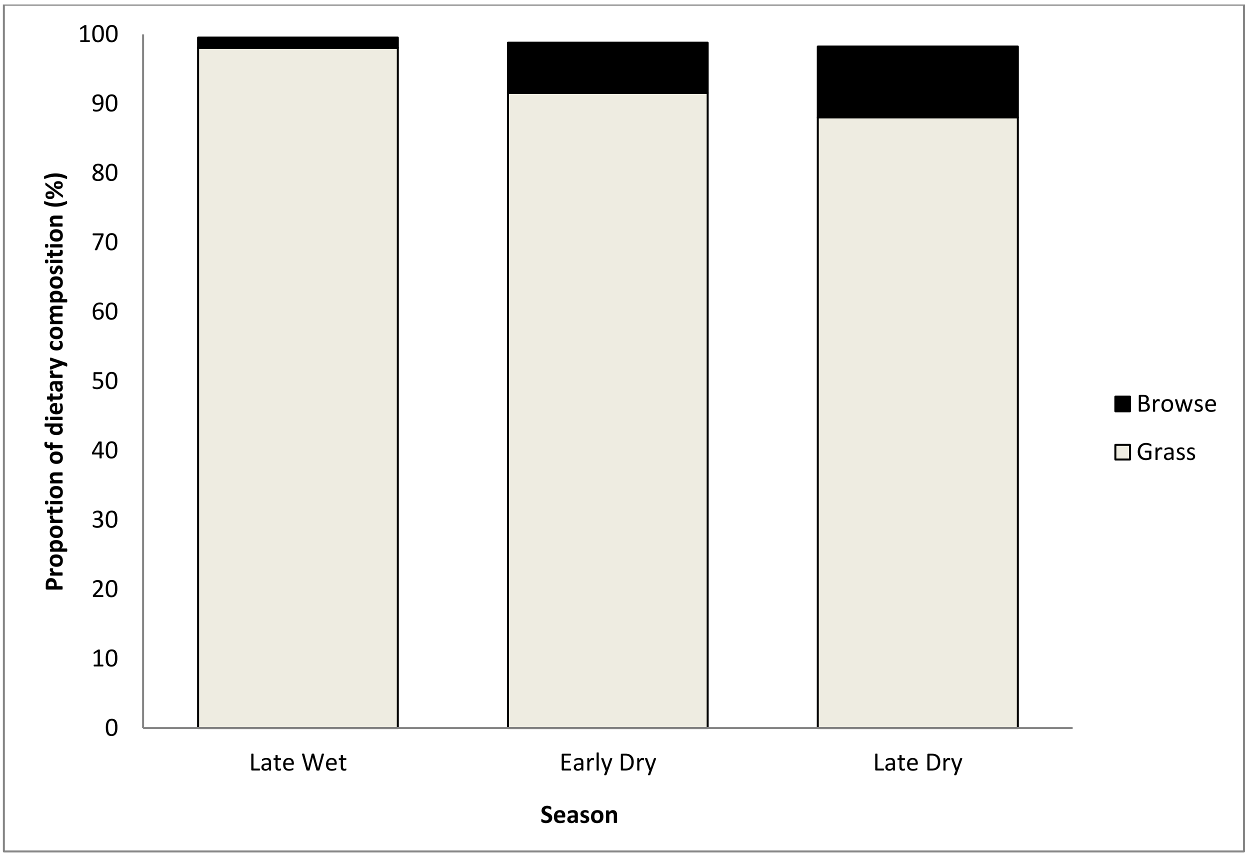

Figure 3.2 Percentage grass and browse consumption for plains zebra (E*quus quagga*) during the late wet season, early dry season and late dry season in Majete Wildlife Reserve, Malawi

3.5 Discussion

The mean $\delta^{13}C$ values of the most widespread C_4 grasses and C_3 browse species was -12.86‰ and -29.11‰ in faecal samples of plains zebra at MWR. This corresponds to the findings of previous studies that have reported a range of -10 and -15‰ for the $\delta^{13}C$ values of subtropical C_4 grasses and -22 and -35‰ for subtropic C_3 browse species (Cerling *et al.*, 1999). Since the isotope values of nitrogen are more complex than the isotope values of carbon as a result of nitrogen fixation and fractionation being affected by environmental factors, our current understanding regarding $\delta^{15}N$ values of plants and faecal matter is limited. In addition, it has been advised to not interpret and analyse $\delta^{15}N$ values until the current understanding regarding nitrogen isotopes has been improved, so therefore the $\delta^{15}N$ values obtained from the analysis of both the plant and faecal samples is not discussed (Sandberg *et al.*, 2012).

The diet of plains zebra in MWR almost entirely consisted of C_4 grasses (84.0 - 100.0%). This is comparable to the findings of other studies conducted on the diet of plains zebra in Addo Elephant Park, Hluhluwe-iMfolozi Park, Kruger National Park and Timbavati area, South Africa, as well as Etosha National Park, Namibia, which have found that grazing can comprise 76 - 100% of the diet. This confirms that plains zebra are predominantly grazers (Arsenault & Owen-Smith, 2011; Bodenstein *et al.*, 2000; Codron *et al.*, 2007; Havarua *et al.*, 2014; Landman & Kerley, 2001). Unlike ruminant mammals, plains zebra are enabled to predominantly graze, thanks to their specialized digestive system that allows them to eat large quantities of low quality foliage (Schoenecker *et al.*, 2016). In addition, it has been suggested that plains zebra have evolved to predominantly graze on low quality foliage in order to decrease competition with other more selective savanna herbivores through their bulk diet (McNaughton, 1985).

Occasional browsing of small trees and shrubs by zebra was observed at MWR, in particular during the late dry season, when the mean and maximum proportion of browse was slightly above the 10% margin of error as suggested by Codron *et al.* (2007). It has been suggested that in order for plains zebra to maintain sufficient protein levels, especially during drought induced conditions, they will occasionally browse (Berry & Louw, 1982). The protein content of C_3 vegetation is generally higher than C_4 vegetation and therefore during dry seasons C_3 vegetation can sustain metabolic requirements better than C_4 vegetation (Schoenecker *et al.*, 2016). Additionally, the increase in the amount of browse observed during the dry seasons compared to the late wet season can be due to a lack of sufficient grass for plains zebra in MWR during the dry season, especially the late dry season when natural fires occur more often (Forrer, 2016; Spies, 2015). It can also possible be due to the onset of the shoot extension period for miombo savanna woodland trees and shrubs, as this generally takes place from early September until November (late dry season), which appears to be triggered by the rising temperature after August (Chidumayo, 1994). Whereas, the lack of browsing during the late wet season can be a consequence of fresh grass growth, which has a higher nutritional value, lower tannin concentration and greater palatability than many C_3 vegetation types (Cooper & Owen-Smith, 1985; Sukumar & Ramesh, 1992).

Even though our study detected a significant seasonal variation in the proportion of browse consumed, a study conducted by Havarua *et al*. (2014) did not notice a significant difference in the contribution of woody shrubs to the diet of plains zebra. If the availability of grass never declined to the point where browsing was needed in order to sustain protein levels during the study conducted by Havarua *et al*. (2014), no significant difference in the contribution of C_3 vegetation to plains zebra diets would be noticed between the different seasons, since plains zebra prefer to graze. The variation in the availability of grass between the two study sites can be driven by differences in vegetation, rainfall, climate and the occurrence of natural fires.

In comparison to the mountain zebra (*Equus zebra*), it appears that plains zebra will only browse when the quality and quantity of grasses declines (Novellie, Fourie, Kok & van der Westhuizen, 1988; Penzhorn, 1982; Penzhorn & Novellie, 1991). On the other hand, the diet of Grevy's zebra (*Equus gervyi*), which generally occur in more drought-stressed environments, can comprise of up to a 30% C_3 browse during the dry season (Churcher, 1993; Kleine, 2010; Williams, 2002). It can therefore be concluded that changes in the seasonal availability of forage can be responsible for a seasonal difference in the diets of zebras throughout Africa (Schoenecker e*t al*., 2016).

Since plains zebra are primarily grazers, the probability of dietary shifts to include a larger proportion of browse than what has been recorded during this specific study is highly unlikely, as it has been suggested that the higher tannin and other allelochemical levels in C_3 vegetation types can be problematic for grazers (Owen-Smith, 1997). Landman & Kerley (2001) anticipated that "if such shifts are observed, it is predicted that the animals will be under severe nutritional stress and that large-scale die offs can be expected." It is therefore of the utmost importance that herbivore dietary requirements and the predicted responses of animals to overcome environmental variation be incorporated into management planning.

3.6 Conclusion

Despite extensive C_3 browse availability at MWR, zebra demonstrated only moderate dietary plasticity to their reliance on C_4 grasses. As such, careful management of grassland habitat and habitat heterogeneity are essential for the persistence of zebra, especially during severe seasonal conditions. Even though this study has contributed to our understanding of the seasonal dietary preference of zebra in miombo savanna woodland, our understanding can be improved to provide a greater in-depth analysis on the seasonal dietary preference of plains zebra and other species in MWR by addressing the following:

1) Microhistological analyses of faecal samples should be conducted in addition to stable isotope analysis in order to determine the frequency of occurrence of individual plant species, as well as different vegetation groups (Stewart, 1967; Schoenecker *et al.*, 2016). Observational studies, in concert with microhistological studies, could also be used to determine the forages consumed (Schoenecker *et al.*, 2016). Both of these techniques will also be able to assist with determining whether zebra prefer feeding on trees, shrubs, forbs, short grass or long grass species during the different seasons.

2) The quality and relative abundance of plant species in the reserve throughout the different seasons can also be compared to the actual consumption of the species (Spies, 2015). This will allow researchers to determine if zebra and other herbivore species select for the most abundant plant species or if herbivores prefer to graze or browse during certain times of the year due to a change in quality of the different vegetation types.

3) Proportion of graze and browse may vary between the four main habitat types (high altitude woodland, medium altitude woodland, low altitude woodland and savanna) identified in MWR. Determing this can be done by dividing the four habitat types into sampling blocks (taking into account the location of waterholes and size of the habitat). Each habitat type should have at least three sampling blocks and a vegetation analysis should be conducted in each sampling block in both the wet and the dry season. In addition, a minimum of ten faecal samples of zebra or other species need to be collected on a monthly basis in each sampling block. Both the vegetation and faecal samples can then be analysed using stable isotope analysis (Forrer, 2016).

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Chapter Four

Artificial waterhole dependency of plains zebra (*Equus quagga*) in Majete Wildlife Reserve, Malawi

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4.1 Abstract

Wildlife's access to water across Africa is becoming highly limited with changing climate and increases in habitat fragmentation. The provision of water in the form of artificial water points (AWPs) can be used as a management tool to support the persistence of plains zebra (*Equus quagga*) in arid parts of their range in sub-Saharan Africa. This study aimed to determine the seasonal artificial water point utilization of plains zebra within Majete Wildlife Reserve, Malawi. Plains zebra are one of 8 large mammal species reintroduced into Majete between 2004 and 2009, and form part of an establishing complex of herbivores that are distributed across the reserve. Four artificial waterholes were monitored from 1 May 2016 to 30 April 2017 with the use of camera traps and positive sightings of zebra were recorded. While increasing availability to water and allowing wider distribution across an arid reserve, AWPs may also artificially increase interspecific and intraspecific competition within finite spaces. We therefore also investigated the interaction rate between plains zebra and other species at AWPs to better understand possible limitations of AWP benefits to zebra. We found that plains zebra utilized artificial waterholes primarily during daylight hours, peaking at 09:00, 13:00 and 14:00. The frequency of visitations to artificial waterholes were significantly different by season (Chi-square Goodness of Fit Test: $x^2_{(df = 3)} = 1809.12$, $p < 0.001$). Plains zebra sightings (totalling 3017 sightings) at AWPs increased during the dry season (2493 sightings), especially the late dry season (1665 sightings), compared to the wet season (524 sightings). The total interaction rate between plains zebra and other species (n = 59), was influenced by both the group mass of other species ($F_{1,52}$ = 15,67, $p < 0.05$) and a change in seasons ($F_{1,52}$ = 5.63, p = 0.02). This study contributed towards a greater understanding of factors affecting zebra water point usage – especially under changing climatic conditions, as very little data is available on general water point usage of zebra in closed reserves. However, future studies are needed to provide a more in-depth analysis of the seasonal variation in AWP usage of zebra and other herbivores in MWR and will be of use when constructing a water provision policy.

4.2 Introduction

One of the main factors affecting plains zebra (*Equus quagga*) survival and reproduction is access to water (Moehlman, King & Kebede, 2016; Skinner & Chimimba, 2005; Smit, Grant & Devereux, 2007). Access to water is becoming even more highly limited with changing climate and increase in habitat fragmentation (Hulme, Doherty, Ngara, New & Lister, 2001; Moehlman *et al*., 2016).

Throughout history, many plains zebra populations migrated seasonally following an abundance of resources, which contributed to the species maintaining stable populations (Ekernas & Berger, 2016). Today, due to the ever increasing human population and habitat fragmentation, only large ecosystems (for example the Serengeti) allow for the seasonal migration of plains zebra (Ekernas & Berger, 2016; Ogutu, Owen-Smith, Peipho & Said, 2011). Outside of these large ecosystems, habitat fragmentation has resulted in declining plains zebra populations (Moehlman *et al*., 2016). This is mainly due to fencing, agriculture and livestock eliminating the access of water and forage to plains zebra. Plains zebra avoid dehydration and starvation by relying on behavioural strategies, for instance remaining close to water and forage or migrating to resource rich areas (Moehlman *et al.*, 2016; Smit & Grant, 2009). A lack of resources will have negative impacts on the distribution, ecology and conservation of plains zebra, as water and forage are fundamental requirements for their survival (Antrobus, 2014).

With the changing climate, it is predicted that rainfall will decrease throughout Africa and climatic variability will increase, possibly eliminating what access is still available to water and forage (Hulme *et al*., 2001). As resources become more limited, plains zebra will need to occupy larger ranges in order to obtain sufficient water and forage, and consequently the carrying capacity of protected and non-protected areas will be altered (Antrobus, 2014; Bartlam-Brooks, Bonyongo & Harris, 2013; Smit & Grant, 2009). Zebra recruitment rates will also subsequently decrease; as previous research conducted on Grevy's zebra (*Equus grevyi*) has found that if zebra need to travel too great a distance to find adequate water and forage, foals will die (Williams, 1998). If droughts persist and resources remain scarce, zebras may be severely impacted (Moehlman *et al*., 2016; Skinner & Chimimba, 2005). These multiple sources of stress may already be taking a toll on plains zebra, as indicated by their recent change in conservation status from Least Concern to Near Threatened (King & Moehlman, 2016).

Due to combined implications of a changing climate and drastic expansion of the human population, the incorporation of behavioural and demographic knowledge into conservation efforts will be one of the most important tools towards preventing the destructive effects of climate change, habitat fragmentation and resource competition (King, Asa, Plucháček, Houpt & Ransom, 2016). One of the most widely used management interventions is the provision of water to wildlife in the form of artificial water points (AWPs) (Smit *et al*., 2007; Traill, 2003). AWPs are generally used in arid and semi-arid areas to maintain wildlife density by stabilising the unpredictability of the available natural water (Chamaillé-Jammes, Fritz & Murindagomo, 2007). Other benefits of having AWPs are that they can extend the forage range of herbivores and aid in the population increase of water-dependent species (Loarie, van Aarde & Pimms, 2009; Redfern, Grant, Gaylard & Getz, 2005).

However, AWPs can have detrimental consequences for some species. A study conducted in Kruger National Park, South Africa, found that during severe droughts AWPs drew an influx of the more common grazers (especially plains zebra) to areas they generally do not occur in (Harrington, Owen-Smith, Viljoen, Mason & Funston, 1999). The more common grazers out-competed the rare antelope species and attracted more predators to areas where rare antelope species generally were exposed to low predator densities

(Cain, Owen-Smith & Macandza, 2011; Harrington *et al.,* 1999; Owen-Smith & Mills, 2006). AWPs have also been blamed for constant herbivory on surrounding vegetation, resulting in vegetation devastation, as herbivores tend to forage close to water points (Smit *et al*., 2007). It is important that managers are informed on how different AWPs are being utilized within a reserve, so that the distribution of animals and impact on the surrounding vegetation can be predicted and evaluated (Smit *et al*., 2007).

Located in southern Malawi, Majete Wildlife Reserve is a fenced reserve, with limited access to surface water and a semi-arid climate. From 2004 to 2009, 8 large mammals of 12 species were reintroduced to the reserve, and have since expanded their distribution throughout the reserve as resources allow. Due to the surrounding communities supporting over 140 000 people, the opportunity for the expansion of Majete is highly restricted. Since the establishment of a public-private partnership (PPP) between African Parks Majete (Pty) Ltd. and the Department of National Parks and Wildlife of Malawi in 2003, 10 solar powered AWPs were installed in Majete over several years to provide the established and reintroduced wildlife with access to water, especially during the dry season (Forrer, 2016; Wienand, 2013).

The aim of this study was to determine how plains zebra (hereafter referred to as zebra) utilised artificial waterholes located within Majete Wildlife Reserve and to determine if there is seasonal variation in such usage. We also aimed to identify the frequency and direction of interspecific interactions at these AWPs to determine if zebra were displaced or time-limited at waterholes due to overt competition. We hypothesised that zebra would prefer to utilize AWPs during day-time and that the utilization of AWPs by zebra would vary between the different seasons, with AWPs being visited more often in the dry season than in the wet season (Ayeni, 1975; Cain *et al*., 2011; Hayward & Hayward, 2012; Sirot, Renaud & Pays, 2016). We hypothesized that interactions would be influenced by species and group sizes encountered (Epaphras *et al*., 2008; Valeix, Chamaillé-Jammes & Fritz, 2007). The results obtained from this study will provide information that can assist the management of Majete with future decisions regarding AWP position or closure. It will also contribute towards a greater understanding of factors affecting zebra water point usage – especially under changing climatic conditions, as very little data is available on general water point usage of zebra in closed reserves (Cain *et al*., 2011).

4.3 Methods

4.3.1 Study site

In the most southern tip of the Great Rift Valley located in southern Malawi, Majete Wildlife Reserve (MWR) covers 700km^2. The vegetation can be divided into savanna, low altitude mixed woodland, medium altitude mixed woodland and high altitude miombo woodland; however, miombo savanna woodland is the main vegetation type of MWR (Forrer, 2016). The Shire River and the Mkulumadzi River defines the northern and eastern boundaries of the reserve and as one progresses from east to west, the altitudinal gradient increases. Steeply undulating hills can be found in the western region of the reserve and there are fewer water bodies in the west than in the east. MWR has approximately seven perennial springs and ten artificial waterholes. A number of small seasonal rivers, temporary pools and springs can also be found, however, these are strongly affected by the seasonal variation in rainfall (Forrer, 2016; Wienand, 2013). The climate is semiarid and the expected rainfall per year is approximately 700 – 1000mm in the west and 680 – 800mm in the east (Forrer, 2016; Gyöngyi, 2011; Spies, 2015; Wienand, 2013). Based on the variation in precipitation, MWR experiences two distinct seasons: the wet season (December – May) and the dry season (June – November) (Forrer, 2016). The average daily temperature is 28.4°C in the summer (December – February) and 23.3°C in the winter (June – August) (Spies, 2015; Wienand, 2013).

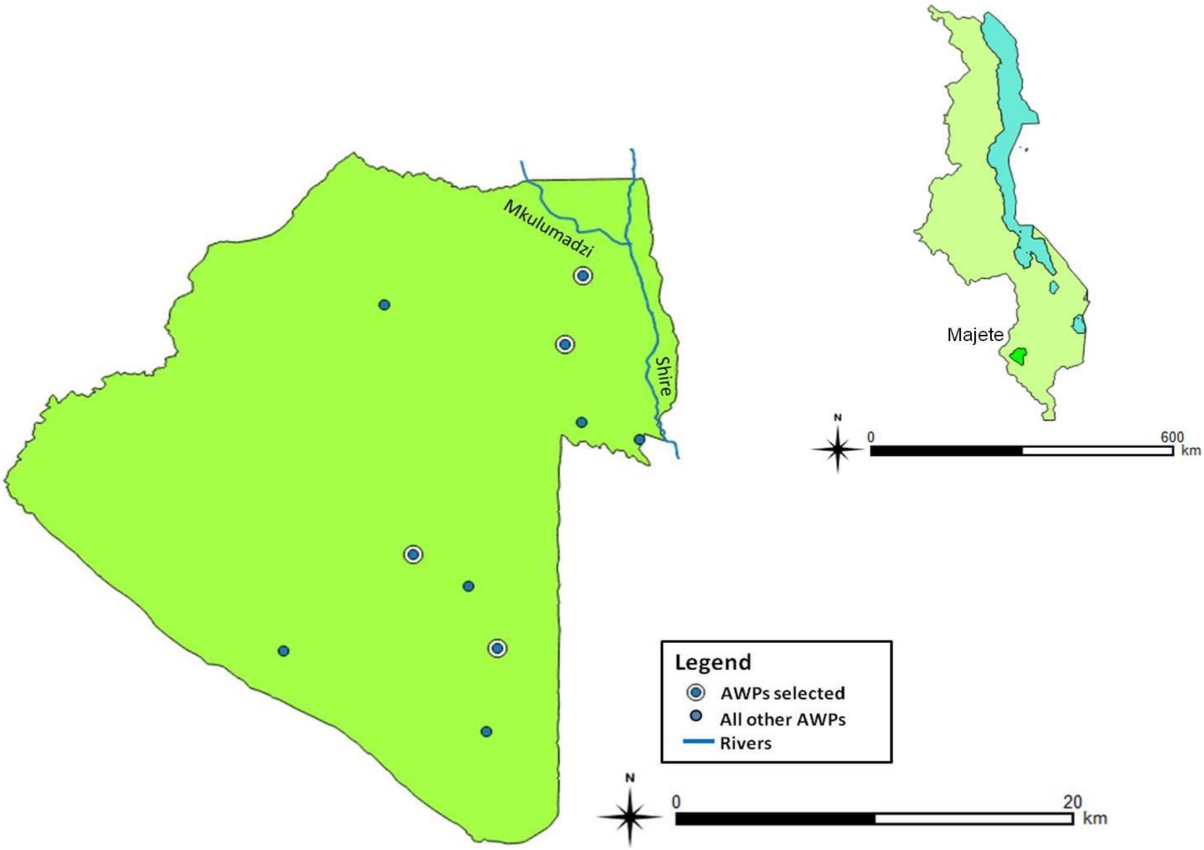

Figure 4.1 The position of Majete Wildlife Reserve in Malawi; and the location of the ten artificial water points (AWPs) and two perennial rivers that occur in Majete Wildlife Reserve. The four AWPs selected for this study are encircled in white (Shapefiles pers. comm. African Parks (Pty) Ltd.)

4.3.2 Artificial waterhole usage

The artificial waterhole usage of zebra within MWR was monitored from 1 May 2016 to 30 April 2017 by installing Cuddeback^{TM} Ambush© camera traps at four AWPs located within the reserve. Camera traps were used instead of observational studies, as they allow for the unobtrusive, nocturnal and diurnal, long-term monitoring of species within their natural environment (Locke *et al*., 2005; Stein, Fuller & Marker, 2008). Two of the AWPs that were monitored were located within the Sanctuary (a 14 000ha site located in the north-eastern region of the reserve) and the other two within the southern region of the reserve, known as Pende. These four AWPs were selected; as the management of MWR was planning to keep these four AWPs running for the entire study period and the aerial survey data from 2015 (African Parks Majete (Pty) Ltd.) indicated that there were high densities of zebra within the areas surroundings these AWPs.

Camera traps were set up on trees/shrubs at previously identified positions that allowed for a wide angle of the waterhole and near visible game paths accessing the AWPs, to ensure the maximum photographic capture of zebra utilizing each AWP. The GPS coordinates of each camera trap was documented in case future repetition was necessary. The Cuddeback^{TM} Ambush© camera traps that were installed were triggered by motion sensors and set to take a single photo, with a delay time of 60 seconds. This was done in order to save battery life and memory space in case a camera was repeatedly triggered by a large herd of animals or by changing vegetation. At night, the cameras made use of a white flash to capture images, thus allowing for 24-hour observations. After every two weeks the camera traps were checked, the 8GB memory cards were replaced with new ones and sufficient battery life was confirmed (if less than 50% batteries were replaced). If necessary, surrounding vegetation was removed in order to prevent grass or tree branches from triggering the cameras.

Immediately after the removal of the memory card, photos were downloaded onto a laptop and saved within a file containing the location and dates. For each zebra sighting (a photograph that contained a portion of or an entire zebra or zebras); time, date (season) and location was recorded. Only positive sightings of zebra were used and any questionable photographs (16 in total) were discarded. Since photographs usually contain only a portion of a herd or a single animal, numbers and group dynamics were not taken into account. The total zebra sightings data collected at the four AWP was separated into location, hourly intervals over 24 hours, as well as four distinct periods: early wet season (December – February), late wet season (March - May), early dry season (June – August) and late dry season (September – November).

4.3.3 Species interaction observations

Camera traps have their limitations and interaction data collected from camera traps proved unreliable for determining the nature of behaviour, group size and all species present (Ancrenaz, Hearn, Ross, Sollmann & Wilting, 2012). Therefore, data on the interactions of zebra with other species at artificial waterholes were collected in person during 12 hour periods (06:00 – 18:00) from May 2016 to April 2017 (two to four days of each month). Observations were conducted at AWPs from either a blind or a vehicle. In order to prevent observers from drawing the attention of zebra and other species, observations were conducted from distances that did not draw the animal's attention and the observers remained as quiet and still as possible. The geographical (GPS coordinates and elevation), temporal (time, date and season) and climatic data (temperature, precipitation and cloud cover) were also collected for each session.

On observing zebra approaching an AWP, the band size and composition (bachelor or family group) was documented. When other species were observed to be present at the AWPs during the same time as zebra, their group size was recorded. A Canon D700 DSLR camera was used to video record the interactions between zebra and other species to allow for the accurate documentation of the interactions via all-occurrence data collection. Interactions with other animals were recorded as either neutral interactions (interactions initiated by either zebra or other species that did not result in the costly modification of either zebra or other species behaviour), interactions from other species towards zebra (interactions that were initiated by other species and resulted in the costly modification of zebra's behaviour) or interactions from zebra towards other species (interactions that were initiated by zebra and resulted in the costly modification of another species behaviour). For example, if a zebra that was drinking at the waterhole looked up due to the approach of another species but continued drinking thereafter, it would have been recorded as a neutral interaction. If the zebra however was chased-off by the other species or departed the vacinity of the waterhole due to the approaching species, it would have been recorded as an interaction from other species towards the zebra.

The unit mass of each species that was found to have interacted with zebra at the artificial waterholes was obtained from Cumming and Cumming (2003), except for lion and baboon which was obtained from Hayward, O'Brien, Hofmeyer and Kerley (2006).

4.3.4 Statistical analyses

All statistical analyses were conducted in Statistica version 13.2 (Dell Software, 2016). Chi-Square Goodness of Fit Tests were conducted to analysis if the frequency of visits by zebra to artificial waterholes were significantly different by waterhole, as well as by season and time of day. The frequency of visits was calculated as the number of photographs containing a proportion of, an entire zebra or group of zebra and compared to an extrinsic theoretical expectation. A correspondence analysis was conducted in order to determine if certain seasons corresponded with a different time of day that zebra preferred to utilize artificial waterholes in MWR. In addition, a Chi-square Test for Independence was also conducted to verify if the pattern that emerged with the use of correspondence analysis was significant or not. In order to determine if bachelor groups interacted with other species more frequently at AWPs than did family groups of zebra, a normal approximation test for equality of two proportions was conducted in which the data collected was compared to an extrinsic theoretical expectation. A general linear model was used to determine if the number of interactions initiated per hour towards zebra were dependent on the group size of the initiating species, the unit mass of the initiating species, the group mass of the interacting species, the group size of zebra being interacted with, the band composition (family or bachelor group) of the zebra group and/or the different seasons. A general linear model was also used to determine if total interactions initiated byzebra towards other species per hour were dependent on the same variables as tested against the number of interactions initiated per hour towards zebra.

4.4 Results

4.4.1 Artificial waterhole usage

A total of 3 017 zebra sightings (a photograph that contained a portion of or entire zebra or zebras) were recorded using camera traps between 1 May 2016 and 30 April 2017 at the four artificial waterholes monitored within MWR. These four artificial waterholes were however not visited equally (Chi-square Goodness of Fit Test: $x^2_{(df = 3)} = 509.45$, $p < 0.001$) (Figure 4.2) The numberof visitations to artificial waterholes by season was also significantly different (Chi-square Goodness of Fit Test: $x^2_{(df = 3)} = 1809.12$, $p < 0.001$). Of the 3 017 zebra sightings recorded, 112 were recorded in the late wet season, 828 in the early dry season, 1 665 in the late dry season and 412 in the early wet season (Figure 4.3).

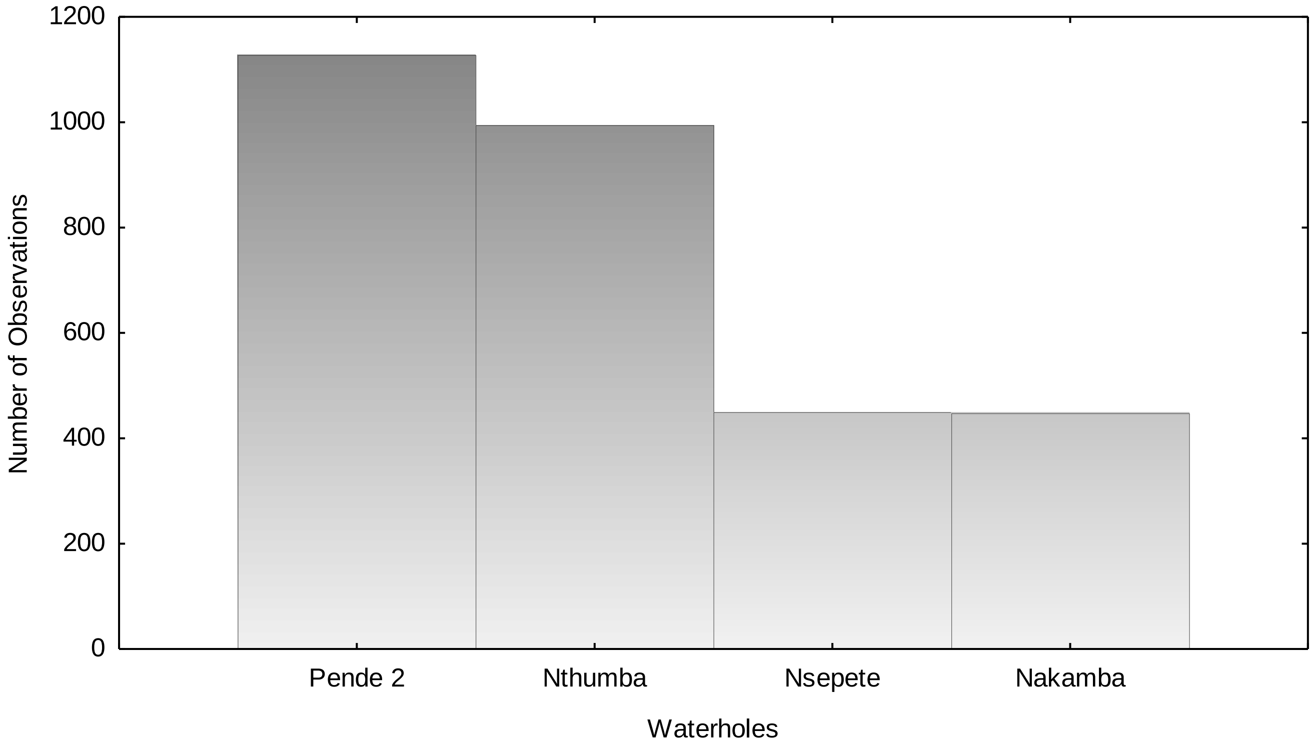

Figure 4.2 The comparative representation of the number of zebra sightings between four different artificial waterholes located within MWR, Malawi (Chi-square Goodness of Fit Test: $x^2_{(df = 3)} = 509.45$, $p < 0.001$)

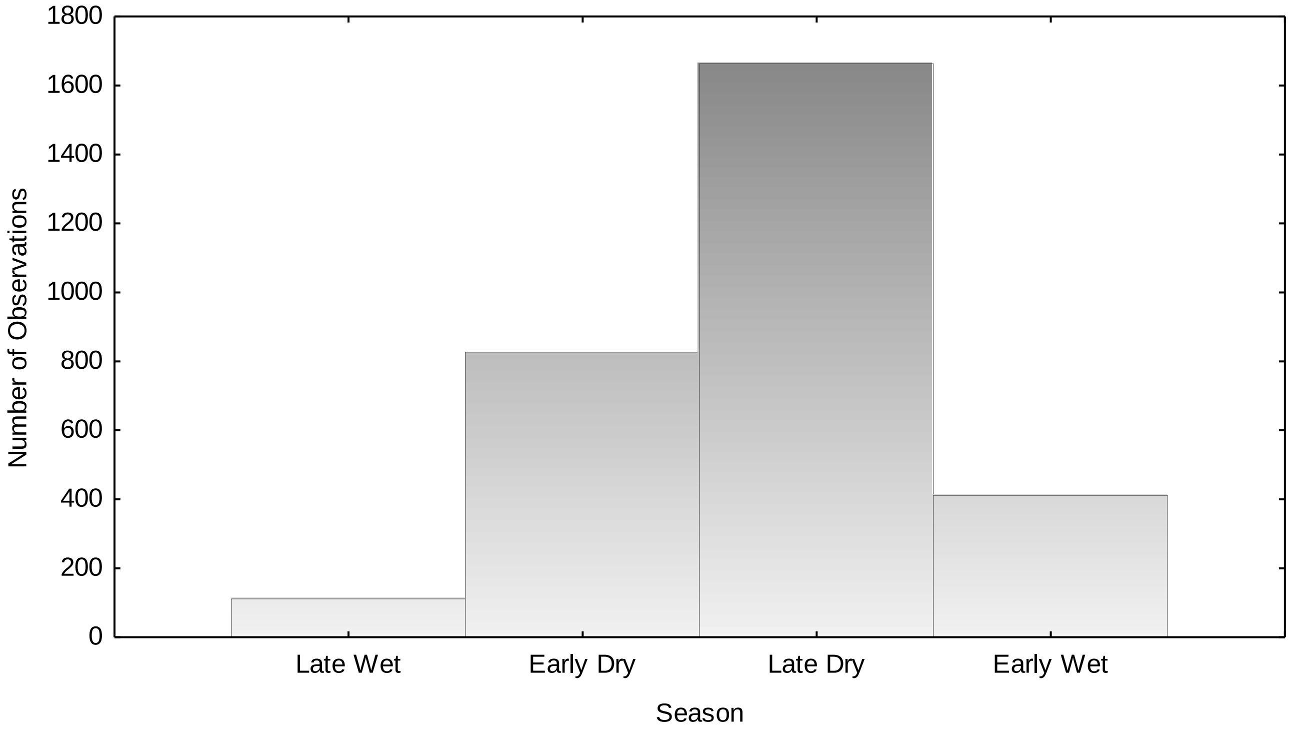

Figure 4.3 The comparative representation of the number of zebra sightings between the different seasons at four artificial waterholes located within MWR, Malawi (Chi-square Goodness of Fit Test: $x^2_{(df = 3)} = 1809.12$, $p < 0.001$)

Zebra were recorded visiting artificial waterholes during each hourly interval over a 24-hour period (Figure 4.4). However, the number of visitations by zebra to artificial waterholes by time of day was significantly different (Chi-square Goodness of Fit Test: $x^2_{(df\ =\ 23)}$ = 2409.19, $p < 0.001$). The majority of zebra sightings were recorded during daylight hours, peaking at 09:00 (296 sightings), as well as 13:00 (323 sightings) and 14:00 (335 sightings) (Figure 4.4). The time of day zebra preferred to visit artificial waterholes however also differed significantly among the four seasons (Chi-square Test of Independence: $x^2_{(df\ =\ 72)}$ = 383.45, $p < 0.001$), with the early wet season showing the strongest correspondence to 09:00, late wet season to 14:00, early dry to 16:00 and late dry to 20:00.

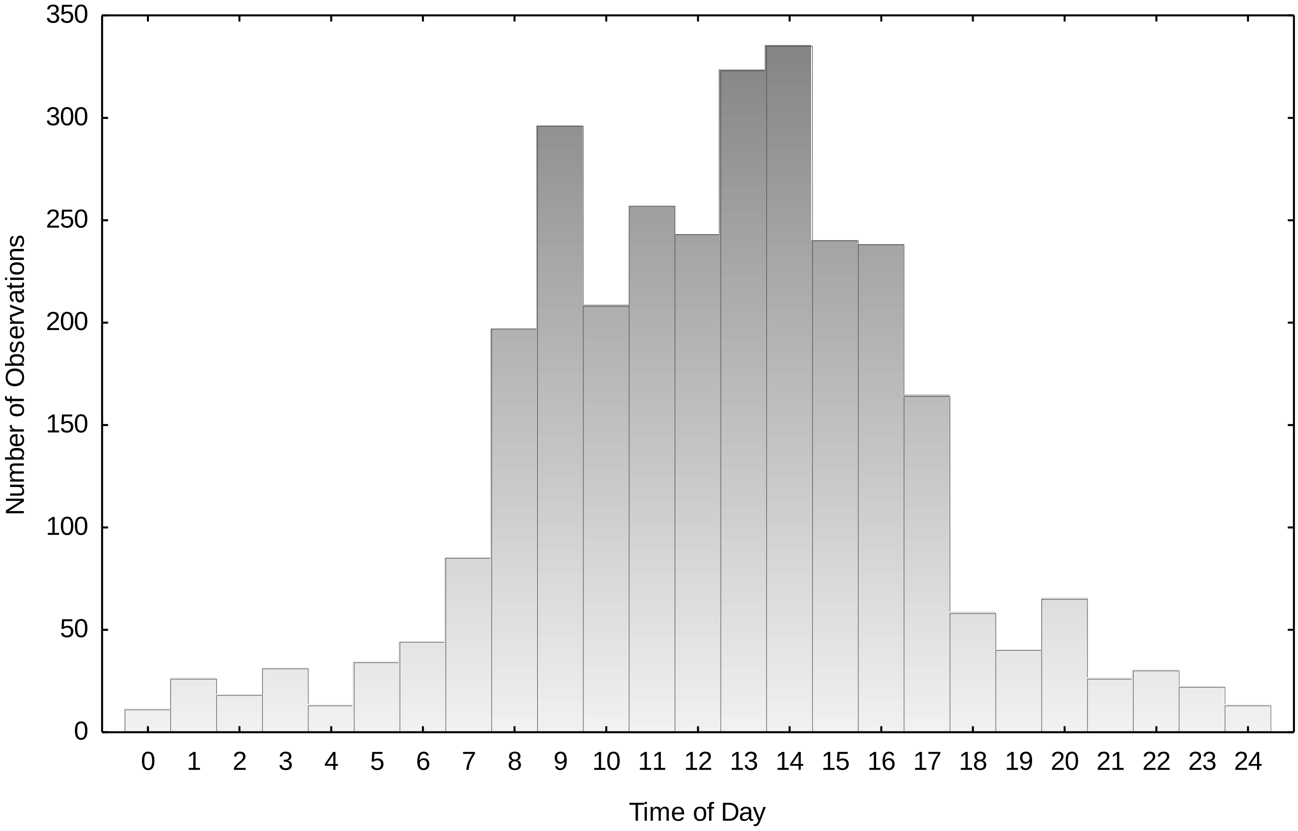

Figure 4.4 The number of zebra sightings recorded accessing artificial waterholes during each hour over 24 hours in MWR, Malawi (Chi-square Goodness of Fit Test: $x^2_{(df = 23)}$ = 2409.19, $p < 0.001$)

4.4.2 Species interactions

A total of 82 interaction observations were recorded of which 12 other species, in addition to other bands of zebra, were observed in association with focal zebra bands (Table 4.1). Five of these species (bushbuck *Tragelaphus scriptus*, kudu *Tragelaphus* *strepsiceros*, lion *Panthera leo*, nyala *Tragelaphus angasii* and sable *Hippotragus niger*) did not interact with zebra even though they were in close proximity (Table 4.1). Zebra only initiated behaviour toward warthog (*Phacochoerus aethiopicus*), waterbuck (*Kobus ellipsiprymnus*), yellow baboon (*Papio cynocephalus*) and other zebra. Buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), elephant (*Loxodonta africana*), waterbuck, warthog, yellow baboon and other zebra all initiated behaviour toward zebra (Table 4.1).

Bachelor groups interacted with other species more frequently than did family groups of zebra (26 of 50 cases of bachelor observations – the number of times zebra were observed occurring with other species at artificial waterholes, were interactions versus 8 of 32 cases of family groups were interactions) (Difference = 0.27 (95% CI = 0.07 - 0.47), Z = 2.49, p = 0.01).

Five species interacted with zebra multiple times (> five occurrences). Of those observations (n = 59), the rate (number of interactions per hour) at which other species initiated behaviour toward zebra was not influenced by either the group size of the initiating species ($F_{1,52}$ = 0.33, p = 0.57) or the group size of the zebra recipient of the behaviour ($F_{1,52}$ = 0.63, p = 0.43). Neither was it influenced by the band composition of the zebra group ($F_{1,52}$ = 1.30, p = 0.26). The rate at which other species initiated behaviour towards zebra was not influenced by unit body mass ($F_{1,52}$ = 0.57, p = 0.46) or group body mass of the initiating species ($F_{1,52}$ = 0.08, p = 0.78). Neither did the change in seasons ($F_{1,52}$ = 0.29, p = 0.59) influence the rate at which other species initiated interactions towards zebra. When investigating the total interaction rate between zebra and the five species that interacted with them more than five times (n = 59), the group mass of other species ($F_{1,52}$ = 15.67, $p < 0.05$), as well as the change in seasons ($F_{1,52}$ = 5.63, p = 0.02) were found to be significant predictors of the total interaction rate. The total interaction rate was not influenced by either the unit mass of the other species ($F_{1,52}$ = 0.10, p = 0.75), group size of other species ($F_{1,52}$ = 0.51, p = 0.48), group size of zebra ($F_{1,52}$ = 0.12, p = 0.73) or band composition ($F_{1,52}$ = 0.41, p = 0.53).

Table 4.1. Interactions (per hour) of zebra with other species at artificial waterholes in Majete Wildlife Reserve, Malawi (2016-2017).

Species	**Number of observations with zebra**	**Group size (Mean ± SE)**	**Group size (Range)**	**Unit mass (kg)**	**Group mass (Mean ± SE)**	**Total interactions (per hour)**	**Number of interactions initiated by zebra (per hour)**	**Number of interactions initiated toward zebra (per hour)**	**Number of neutral interactions (per hour)**
Baboon (yellow)	15	13.9 ± 2.13	3-32	12	167.2 ± 25.54	5.6 ± 2.56	0.9 ± 0.55	1.4 ± 1.19	3.3 ± 2.32
Buffalo	1	1	1	450	450	1.5 ± 1.50	0	1.5 ± 1.50	0
Bushbuck	1	2	2	30	60	0	0	0	0
Eland	2	2.5 ± 1.50	1-4	340	850.0 ± 510.00	2.3 ± 2.25	0	2.3 ± 2.25	0
Elephant	6	7.3 ± 4.43	1-28	1725	12 650.0 ± 7 645.55	12.6 ± 7.39	0	2.5 ± 1.10	10.1 ± 7.90
Hartebeest	1	3	3	137	411	2	0	0	2
Impala	11	9.6 ± 4.32	1-51	45	429.6 ± 194.49	1.9 ± 1.91	0	0	1.9 ± 1.91
Kudu	3	3.7 ± 2.19	1-8	135	495.0 ± 295.09	0	0	0	0
Lion	1	4	4	110	110	0	0	0	0
Nyala	2	1.5 ± 0.50	1-2	73	109.5 ± 36.50	0	0	0	0
Other zebra	2	6.0 ± 1.00	5-7	200	1 200.0 ± 200.00	7.5 ± 7.50	3.8 ± 3.75	3.8 ± 3.75	0
Sable	2	1	1	185	185.0 ± 0.00	0	0	0	0
Warthog	10	3.6 ± 0.58	1-6	45	162.0 ± 26.15	4.3 ± 1.94	1.7 ± 1.14	0.5 ± 0.50	2.2 ± 1.57
Waterbuck	25	9.4 ± 1.30	1-20	160	1 510.4 ± 207.19	4.7 ± 1.61	2.1 ± 1.16	1.4 ± 0.78	1.3 ± 0.59

Note: unit mass was obtained from Cumming and Cumming (2003), except for lion and baboon which was obtained from Hayward, O'Brien, Hofmeyr and Kerley (2006)

4.5 Discussion

In MWR, zebra utilized all four AWPs monitored. The two waterholes located in the southern region of the reserve (Nthumba and Pende 2) were visited more often than the two in the north-eastern region (Nakamba and Nsepete). This is most likely due to higher densities of zebra in the southern region of the reserve than in the north-eastern region (as determined by the aerial survey conducted by African Parks in 2015). The results also indicate that AWPs were primarily utilized during daylight hours. The time of day zebra utilized AWPs corresponds to the patterns reported in other populations (Antrobus, 2014; Ayeni, 1975; Cain *et al*., 2011; Hayward & Hayward, 2012). The preferred diurnal utilization of AWPs in MWR may be due to zebra avoiding the utilization of AWPs at night in order to evade predators as their ability to detect predators is reduced at night (Ayeni, 1975; Hayward & Hayward, 2012; Sirot *et al*., 2016). Interestingly, Hayward and Hayward (2012) found that zebra never visited waterholes at night; however zebra were observed to occasionally visit AWPs after dark in MWR. The occasional utilization of AWPs after sunset may be as a response to predator densities far below the carrying capacity of the reserve (Briers-Louw, 2017). The occasional visits to AWPs after dark may also be as a result of heat stress (Hayward & Hayward, 2012). Strong interspecific competition over water during the day may also explain why zebra in MWR occasionally utilized AWPs at night (Sirot *et al*., 2016).

Daytime AWP usage by zebra within MWR peaked at 09:00, 13:00 and 14:00. This corresponds to studies conducted in Tsavo National Park and Lewa Conservancy, Kenya, as well as Kruger National Park, South Africa and Hwange National Park, Zimbabwe, which also observed the daytime AWP usage of zebra to peak at these specific times (Ayeni, 1975; Cain *et al*., 2011; Rubenstein, 2010; Valeix *et al*., 2007). However, zebra visited AWPs at different time of day in different seasons in MWR. When the natural surface water was most abundant (late wet season) and competition over AWPs consequently lower, zebra preferred to utilize AWPs at 14:00. As the availability of natural surface water diminished and competition over AWPs increased (early dry season) zebra visited AWPs more often at 16:00. The added pressure of heat stress and further increases in interference competition during the late dry season resulted in zebra displaying an increase in visitations to AWPs at 20:00. During the early wet season the arrival of the rain allows natural surface water availability to increase, temperatures start to cool and consequently competition for water decreases, allowing zebra to shift their drinking time to 09:00. The seasonal change in utilization of AWPs by zebra in MWR indicates that an increase in interference competition, as a result of natural water sources becoming limited and animals aggregating around AWPs, may result in zebra drinking at a different time period to avoid interspecific competition around these waterholes with more competitive species (species with a larger group body mass, for example elephants: Cain *et al*., 2011; Sirot *et al*., 2016; Valeix *et al*., 2007). Furthermore, it can also indicate that heat stress affects the utilization of AWPs, as travelling to drink during the middle of the day can become costly from a thermoregulatory point of view – since temperatures can reach as high as 50°C in the late dry season in MWR (Bell, 1984; Sirot *et al*., 2016). This corresponds to the findings of another study conducted in Hwange National Park, Zimbabwe, in which thermoregulation was noted as an important factor influencing the time spent accessing water (Valeix, Fritz, Matsika, Matsvimbo & Madzikanda, 2008).

Zebra sightings at AWPs increased drastically during the dry season, especially the late dry season, compared to the wet season sightings at AWPs. This corresponds to the findings of other studies (Ayeni, 1975; Cain *et al*., 2011; Valeix *et al*., 2008). The increase in zebra AWP utilization during the dry season can be as a consequence of natural surface water becoming limited to a few perennial sources during the dry season in MWR (Bell, 1984). There is a strong seasonal variation in rainfall within MWR; with the majority of rainfall occurring in the early wet season – explaining why only 4% of the total sightings of zebra at AWPs occurred during this season. Likewise, the increase in zebra sightings at AWPs during the dry season can also be as a result of zebra drinking more frequently during the dry season in order to meet their physiological requirements – as the water content of grasses decrease during the dry season, resulting in zebra not acquiring sufficient moisture from their food (Epaphras *et al*., 2008; Smit *et al*., 2007; Western, 1975). Hence artificial waterholes act as an important source of water for zebra during the dry season in MWR.

An increase in zebra at AWPs during the dry season can cause habitat over-utilization and degradation around AWPs (Ayeni, 1975; Cain *et al*., 2011; Chamaillé-Jammes, Charbonnel, Dray, Madzikanda & Fritz, 2016). If the waterhole distribution is uniform across the landscape, vegetation degradation around waterholes has the potential to cause habitat homogenization and consequently system resilience will be compromised resulting in starvation induced mortalities especially during serious drought conditions (Chamaillé-Jammes *et al*., 2016; Smit & Grant, 2009). An influx of zebra at AWPs during the dry season can also result in an increase in predation around AWPs during the dry season, consequently increasing the predation pressures on low-density antelope, as predators were more often seen at AWPs during the dry season (Cain *et al*., 2011; Sirot *et al*., 2016; Smit & Grant, 2009). It can also result in an increase in competition between zebra and other species for the utilization of AWPs (Epaphras *et al*., 2008; Smit & Grant, 2009).

Results from this study indicated that a change in seasons acted as a significant predictor of the total interaction rate between zebra and other species. Confirming that, as previously discussed, a decrease in natural surface water availability with the progression of the wet to the dry season will cause animals to aggregate around AWPs and increase interspecific competition between zebra and other species (Cain *et al*., 2011; Sirot *et al*., 2016; Valeix *et al*., 2007). The group mass of the interacting species was found to be a strong, significant predictor of the total interaction rate between zebra and other species. This agrees with the findings of other studies, as larger species and groups benefit from a direct size advantage and tend to be more dominant at waterholes – evicting groups with a smaller mass through interference competition or causing other species to approach water sources more cautiously (Sirot *et al*., 2016; Valeix, Fritz, Canévet, Le Bel & Madzikanda, 2009).

However, neither a change in seasons nor group mass of the interacting species had a significant effect on the rate of interactions towards zebra. This could be due to the small sample size of the study since both season and group mass had a significant effect on the total interaction rate. Zebra may have avoided interspecific competition directed towards them by shifting their activity patterns at AWPs, resulting in a non-significant relationship between the rate of interactions towards zebra and a change in seasons (Valeix *et al*., 2007). It was observed that bachelor groups interacted more frequently with other species at AWPs than did family groups. To our knowledge no other study has evaluated this phenomenon. Family groups may minimize their time spent at waterholes in order to reduce the risk of exposing foals to predatory species or interference competition, given that other studies have observed that waterholes often correspond to high predation risk and increased interference competition as a result of resource crowding (Sirot *et al*., 2016;

Smit & Grant, 2009; Valeix *et al*., 2009). Bachelors might increase their time spent around AWPs in order to increase the probability of encountering family groups so that they can attempt to obtain a female of their own. Further investigation is needed in order to determine why bachelor groups interacted more frequently with other species at AWPs than did family groups.

4.6 Conclusion

In order to overcome the shortage of natural surface water during the dry season since no rainfall occur during this time of the year, the provision of water in the form of AWPs in MWR is crucial to prevent mortalities of zebra and possibly other water-dependent species, especially water-dependent grazers (Epaphras *et al*., 2008; Owen-Smith, 1996). The increase in zebra sightings at artificial waterholes during the dry season also demonstrates the importance of AWPs toward ensuring the future persistence of plains zebra in arid and semi-arid regions of Africa, given climate change predictions of a decrease in rainfall for southern and eastern Africa and an increase in climatic variability, and consequent limited access to natural surface water (Hulme *et al*., 2001). However, it is important to note that the provision of surface water also has the potential to uncouple zebra and other herbivore populations from their natural limitations regulating population size (Farmer, 2010). It can result in habitat degradation, increased competition and predation around AWPs (Chamaillé-Jammes *et al*., 2016; Sirot *et al*., 2016; Smit & Grant, 2009).

The results of this study suggest that competition may influence waterhole usage by zebra in MWR. The establishment of AWPs has likely allowed zebra to distribute themselves farther away from natural water sources (rivers, springs and temporal pools) and thus disperse grazing across the reserve. However, to assist managers and conservation agencies in ensuring the future of plains zebra and other water-dependent species, a justifiable water provision policy is needed based on scientifically sound research that incorporates a holistic approach to enhance ecosystem resilience (Smit & Grant, 2009). Therefore, future studies are needed to provide a more in-depth analysis of the seasonal variation in AWP usage of zebra and other herbivores in MWR. Future studies should investigate and improve on the following:

1) Seasonal variation in the utilization of natural water sources needs to be compared to the seasonal utilization of AWPs. The distance between these sources needs to be mapped and accounted for, as well as the seasonal difference in surface water availability in order to provide more accurate guidelines for artificial waterhole provision (Owen-Smith, 1996; Redfern *et al*., 2005). This can be done by conducting counts during the wet and the dry season in which both surface-water and herbivore distribution data can be collected simultaneously (Smit & Grant, 2009).

2) The presence of crocodiles in the two main rivers might influence AWP usage by zebra and other herbivores and result in animals preferring water sources without crocodiles present (Steer & Doody, 2009). This will need further investigation.

3) The quality of water sources needs to be investigated in order to untangle the particular role of water quality in driving herbivore utilization of waterholes (Chamaillé-Jammes *et al*., 2016). This can be done by measuring the pH, salinity, mineral composition, dissolved oxygen concentration and surface water temperature of water sources (Antrobus, 2014; Epaphras *et al*., 2008; Wolanski & Gereta, 2001). The extent of algae blooms at each source, as well as the possibility of water sources carrying diseases and pests should also be determined (Ayeni, 1975; Epaphras *et al*., 2008). These results should be taken into account when quantifying water source preference of different species (Epaphras *et al*., 2008).

4) Habitat selection can also influence herbivore abundance at waterholes (Chamaillé-Jammes *et al*., 2016; Redfern *et al*., 2005). When determining the utilization of water sources by herbivores, the topography, elevation, soil composition and vegetation (type, structure and cover) around each water source needs to be determined and taken into account as possible factors that might influence and shape the distribution of species and ultimately act as a driver towards which water sources are being utilized more often than others (Antrobus, 2014; Chamaillé-Jammes *et al*., 2016; Farmer, 2010; Rubenstein, 2010).

5) It is well known that herbivores aggregate around surface water, especially during the dry season or droughts; and that these high herbivore pressures often lead to piosphere effects, vegetation degradation and landscape homogeneity (Chamaillé-Jammes *et al*.,

2007; Chamaillé-Jammes *et al*., 2016). It is important to quantify the rate and intensity of vegetation destruction around the water sources as a result of herbivore pressures (Ayeni, 1975). This can be done with the help of satellite imagery or fixed-point photography (Farmer, 2010; Tafangenyasha, 1997; Trollope, Trollope, Biggs, Pienaar & Potgieter, 1998; Wienand, 2013).

6) The travelling distance between water and forage needs to be investigated as it will determine if forage or water is the main factor driving the distribution of herbivores. This will also allow conservationists and management to determine if the spacing of artificial waterholes will allow for a heterogenic landscape, as well as sufficient reserve grazing during drought conditions (Owen-Smith, 1996; Smit *et al*., 2007). The travelling distance between water and forage can be investigated by conducting aerial counts or by radio-collaring individuals from different species (Cain *et al*., 2011; Grant, Davidson, Funston & Pienaar, 2002; Smit *et al*., 2007).

7) AWPs have the potential to alter predator-prey relationships (Chamaillé-Jammes *et al*., 2016). In order to monitor this effect one can radio-collar predators and herbivores to determine if the opening or closing of AWPs result in a shift in their movement patterns (Cain *et al*., 2011). Waterholes can also be monitored to determine if prey shift their behaviour around waterholes under different risks of encountering predators (Valeix *et al*., 2009). Game-theoretical models that are founded on evolutionary algorithms can investigate the change in herbivore temporal patterns around waterholes under different predation pressures as a result of AWP opening or closure (Sirot *et al*., 2016).

8) Lastly, there is a need to quantify the variability of surface water availability as a result of climate change over an interannual time scale (Chamaillé-Jammes *et al*., 2007; Smit & Grant, 2009).

4.7 Acknowledgements

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Chapter Five

Time budget & social behaviour of plains zebra (*Equus quagga*) in Majete Wildlife Reserve, Malawi

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5.1 Abstract

Plains zebra (*Equus quagga*) were reintroduced to Majete Wildlife Reserve, Malawi, from 2004 to 2009. The incorporation of behavioural knowledge into such conservation efforts is becoming an important tool towards preventing the destructive effects of habitat fragmentation and resource competition – as studying animal behaviour allows us to gain an insight on how groups function and individuals react. The aim of this study was to quantify the daylight time budget and social interactions of both family and bachelor bands of plains zebra now that the Majete population has grown and become established. We found that feeding occupied the largest percentage (mean = 41.8% ± 2.36 [SE]) of family band daylight time budgets, followed by resting (18.5% ± 2.21), locomotion (10.9% ± 1.05), vigilance (7.5% ± 0.92), maintenance (2.7% ± 0.92) and social behaviour (1.4% ± 0.33). Bachelor bands spent the majority of their time being vigilant (27.0% ± 2.72), followed by locomotion (21.0% ± 2.05), feeding (18.4% ± 2.32), resting (15.4% ± 2.85), maintenance (6.4% ± 1.86) and social behaviour (2.4% ± 0.68). Non-agonistic social behaviour was observed at a rate of 6.1 times/hour in bachelor bands compared to a rate of 2.3 times/hour in family bands; and agonistic events 1.8 times/hour in bachelor bands and 0.5 times/hour in family bands. Differences in behaviour between family and bachelor bands suggest that social interactions play an integral role in group stability and structure, as well as how individuals in groups

allocate their time between vigilance and subsistence. Our results suggest that the daylight time budgets of plains zebra are influenced by their environment, energy requirements, social structure, and predation pressures. Seasonal variation in time spent feeding was detected and may be the consequence of a behavioural change to more nocturnal activity or could indicate lack of adequate forage availability.

5.2 Introduction

Behavioural ecology is based on the fundamental idea that an animal's behaviour is a product of the features of their environment (Krebs & Davies, 1997). Therefore, changes in the environment should lead to changes in behaviour; otherwise it will result in lower reproductive physiology and/or death (Rubenstein, 2010). Changes in behaviour can also lead to changes in the environment, for example, resource availability can be influenced and shaped by individual actions (Sibly & Smith, 1985). It is thus hypothesized that the social organization of the plains zebra (*Equus quagga*) has evolved to overcome social and ecological problems, such as resource availability, bachelor harassment and predator pressures (Rubenstein & Hack, 2004).

During the last century the social organization and population ecology of the plains zebra (hereafter referred to as zebra) was documented by numerous authors (Fischhoff, Dushoff, Sundaresan, Cordingley & Rubenstein, 2009; Fischhoff *et al.*, 2007; Fischhoff, Sundaresan, Cordingley & Rubenstein, 2007; Gasaway, Gasaway & Berry, 1996, Goargiadis, Hack & Turpin, 2003; Klingel, 1969; Rubenstein, 1994, 2010; Rubenstein & Hack, 2004). These studies observed a two-tiered social organization for zebra: firstly, core social groups consisting of one male and many females (or many males without their own females) form bands, and secondly bands can merge together to form temporary herds (Fischhoff *et al.*, 2007a; Hack, East & Rubenstein, 2002; Klingel, 1969; Rubenstein, 2010). Even though the social organization and population ecology of zebra has been thoroughly investigated, only one long-term observation of the behaviour of individual plains zebra in the wild has been conducted (Simpson, Rands & Nicol, 2012). Other behavioural studies on zebra have either been short term (Neuhaus & Ruckstuhl, 2002), or only specific behavioural aspects were studied (Brooks & Harris, 2008; Fischhoff *et al.*, 2007a). Few studies on zebra have rigorously quantified behaviour. In contrast, the behaviour of other species (for example the

African elephant *Loxodonta africana* and chimpanzee *Pan troglodytes*) has been meticulously investigated by numerous long-term studies (Simpson *et al*., 2012). These longitudinal studies have revealed characteristics overlooked by population-level studies and have strengthened our understanding of these species, as well as improved conservation strategies to ensure their continued existence (Simpson *et al*., 2012). Similarly, long-term studies on the behaviour of zebra can accomplish the same.

The incorporation of behavioural knowledge into conservation efforts is becoming an important tool towards preventing the destructive effects of habitat fragmentation and resource competition – as studying animal behaviour allows us to gain an insight on how groups function and individuals react (King, Asa, Plucháček, Houpt & Ransom, 2016; Rubenstein, 2010). This will aid conservation as it provides a key to understanding and ensuring the future welfare of animals and enables scientists to address both theoretical and applied questions, for example behavioural changes related to fertility control or post-reintroduction (King *et al*., 2016; Ransom & Cade, 2009;). It can also be of significant value when dealing with a species' influence and position in an ecosystem (Buchholz, 2007; Ransom & Cade, 2009; Sutherland, 1998). If conservationists could decode the rules governing how animal behaviour is shaped by environmental features, they could enhance the survival prospects of animals by intervening and manipulating the link by either improving ecosystem functioning or by altering human behaviour (Rubenstein, 2010).

One of the methods used to study the behaviour of animals is quantifying time budgets, and is defined as "... a day in the life of an animal broken down into different behaviours based on an ethogram" (King *et al*., 2016). Time budgets require discretely defined categorical behaviours in order to quantify each unique behaviour in terms of proportion of time exhibited or a count of occurrences. Time budgets also require a protocol stating explicitly which behaviours take precedence in data recording when more than one behaviour occurs simultaneously (Ransom & Cade, 2009). Several techniques as described by Altman (1974), can be used to attain the collection of ethological data. However, instantaneous scan sampling at one minute intervals was found to be ideal for quantifying time budgets during a study conducted on feral horses (*Equus caballus*), which organize themselves similarly to zebras (Ransom & Cade, 2009). Instantaneous scan sampling does have the potential to overlook infrequent and briefly expressed behaviours (Doran, 1992; Houpt, 1991). This problem can be overcome by using either the all-occurrence method or focal sampling (Ransom & Cade, 2009).

This study aimed to examine the behaviour and social interactions of zebra in Majete Wildlife Reserve (MWR) through the use of time budgets. We hypothesized that the daylight time budget behaviours of zebra would be influenced by their sex, age, foal presence, body condition and/or group size, and the time of day and season. We also hypothesized that family bands would display more social interactions than bachelor bands. Since the reserve was fenced, migration was impossible, thus allowing for multiple observations of a closed population over a 12-month period. The ultimate objective of this study was to assist management and conservation agencies in ensuring the future persistence of zebra in MWR more than 13 years after their initial reintroduction by incorporating better knowledge of behavioural ecology.

5.3 Methods

5.3.1 *Study site*

MWR is located in southern Malawi's Lower Shire Valley region and covers 700km^2. The reserve has a semiarid climate and receives an expected rainfall of 680 - 1000mm a year, of which the majority occurs between December and April (Gyöngyi, 2011; Spies, 2015). Temperatures average at 23.3°C in the winter (June to August) and 28.4°C in the summer (December to February) (Gyöngyi, 2011; Spies, 2015; Wienand, 2013). MWR has a strong altitudinal gradient that increases from east to west and the two main perennial rivers, the Shire River and Mkulumadzi River, mark the northern and eastern boarders. There are also ten artificial water points (AWPs) located within the reserve and blinds overlook two of these AWPs (Forrer, 2016; Wienand, 2013). The vegetation is classified as miombo savanna woodland and can be divided into four distinct classes: savanna, high altitude miombo woodland, medium altitude woodland and high altitude woodland (Forrer, 2016).

In 1955, MWR was declared a game reserve, however high levels of poaching and a lack of law-enforcement resulted in the eradication of majority of the large mammals from the reserve by the mid-1990s (Gyöngyi, 2011; Sherry, 1989). In 2003, African Parks Majete (Pty) Ltd. and the Malawian Department of National Parks and Wildlife (DNPW) established a public-private partnerships (PPP) in which they aimed to rehabilitate MWR. Since then, the reserve has been completely fenced off and 14 different mammal species (over 2550 animals) were reintroduced (including 174 plains zebras), making it one of Africa’s largest wildlife reintroductions to date (Forrer, 2016; Spies, 2015; Wienand, 2013).

5.3.2 *Behavioural sampling*

Behavioural observations to determine the time budgets of zebra were conducted in MWR between 08:00 and 20:00 over a 12 month period (22 April 2016 – 14 April 2017). Observations were either conducted on foot, from a vehicle or a blind. All observations conducted on foot or from a vehicle were conducted from distances that did not draw the attention of the zebra to the presence of the observer. When conducting observations from a blind, the observers were responsible for not drawing the attention of the zebra, by remaining as quiet and still as possible. During each observation session, temporal (time and date), geographic (GPS coordinates and elevation) and climatic data (temperature, precipitation and cloud cover) were documented at the start of the observation. The approximate distance of each observation, as well as the band size, band ID and band composition was also recorded (see datasheet used to collect data in Appendix 3).

Photographs of the group as a whole and each individual zebra, were taken with a Canon D700 DSLR camera. This allowed for the individual identification of each zebra by comparing their unique stripe patterns on their right and left sides to photographic records of the reserve’s zebra and allowed for additional photographic records of newly identified individuals and bands. Since each zebra was identified in all of the behavioural sessions conducted, the activities of specific individuals could be documented. The sex of each zebra was determined by examining their genitals, and the age class of each zebra was recorded as either: foal (0 - 12 months), yearling (12 - 24 months) or adult (more than 24 months). The methods as described by Klingel (1969) were used to determine their age. Foal presence or absence was documented for adult females, and a body score was ascribed to each individual observed in every behavioural session. The body scoring system developed by Henneke, Potter, Kreider and Yeates (1983) was used to accurately assign body scores. Once all of the above mentioned information was documented, behavioural observations were recorded by digital video using a Canon D700 DSLR camera for as long as zebra could be followed as required by the focal sampling protocol. A behavioural session needed to be more than fifteen minutes long in order to be included into the data and the longest behavioural session recorded lasted 80 minutes.

The video footage was then analysed to study the time budgets of each individual zebra present within a bandvia instantaneous scan sampling at one minute intervals. In other words, at every one minute interval the behaviour at that specific point in time for each individual within the band was recorded. Specific behaviours were defined and categorized into a set of nine mutually exclusive time budget categories according to the ethogram of Ransom and Cade (2009) and Ransom, Cade and Hobbs (2010). This enabled us to accurately record the different behaviours observed. The categories were: feeding (grazing, coprophagy, soil ingestion, suckling and pawing at food source), drinking, locomotion (walking, trotting, running and swimming), resting, (standing, sleeping, lying down, getting up, yawning and stretching), maintenance (grooming, comfort and excretion), vigilance (standing attentive), social (herding, harem tending, reproductive, aggression, submission and harem social), interaction with other animals, and unknown behaviour (interaction with humans and out of sight). In the rare case that an animal was observed doing two things at once, the predominant behaviour was recorded.

Since instantaneous scan sampling can underestimate rare events, all-occurrence data collection using the same video footage as above, was used to collect data on social behaviours. Specific social behaviours were defined and categorized into a set of twenty-two discrete categories according to the ethogram of Ransom and Cade (2009). The categories were: herding (snaking or driving), defending females, recruiting females, copulation successful, copulation unsuccessful, copulation forced, parturition, estrous, female acceptance, female rejection, male reproductive tending, aggression 1 (threat), aggression 2 (bump or push), aggression 3 (chase), aggression 4 (kick, stomp or bite), aggression 5 (rear), aggression 6 (strike), aggression 7 (box), submission, non-agonistic social, mutual grooming or female-female urine marking. These twenty-two distinct social events were then further categorized as either affiliative or agonistic behaviour as according to King *et al.* (2016). According to King *et al*. (2016) affiliative behaviour is the “non-agonistic interactions between two individuals that appear to promote stable relationships” and agonistic behaviour is the "interactions resulting in increased distance between two individuals, either through defensive or aggressive behaviour."

5.3.3 *Statistical analysis*

Time budget data were collected through 1-min scan sampling of each individual zebra observed, and as such those data were not independent; therefore, we aggregated all minutes of each behaviour observed per individual per observation session and divided those values by time observed (15 to 80 minutes) to generate a proportion for each behaviour detected. Likewise all-occurrence social behaviours were transformed into proportions by summing the count of events within an observation session and dividing by the duration of observation. The dependent variable in all models was thus a proportion by independent observation session.

All individual zebra present in a given band being observed were sampled, but neither bands nor individuals were sampled equally across the entire study due to the nature of finding bands and ability of individuals to change bands between observations. The repeated and unequal measures were accommodated by incorporating individual identity as a random effect on the intercept of each linear model as described below. This allowed any effects arising from sampling frequency of some individuals to explicitly inform the estimated behaviour. This structure also allowed analyses to include a measure of variability among individuals that would otherwise not be captured (such as variation that might arise from age, experience, temperament, or genetics).

Because time of day is likely to influence some behaviours, we categorized observation time into three discrete periods (08:00 - 12:00h; 12:01 - 16:00h and 16:01 - 20:00h) and included this variable as an independent factor in the models. Some behaviours were also seldomly detected and thus sample sizes were insufficient for modelling, but were functionally similar to other behaviours. We therefore grouped feeding and drinking behaviour into a single category for analysis (hereafter referred to as feeding behaviour), and vigilance behaviour and interaction with other animals into a single category for analysis (hereafter referred to as vigilance). Preliminary analyses indicated that yearlings and adults did not behave differently in any behaviours measured and thus were grouped together for analysis (hereafter referred to as adults).

Time budget data are inherently compositional in nature, such that as any one component increases or decreases, one or more of the other behaviours in the composition must compensate accordingly. Compositional analytical tools do not allow for detailed analyses of the individual behaviors that include the potentially important factors influencing those behaviours. As such, we modelled each time budget behaviour separately but discuss the findings with the context of compositional dependence. We fitted separate models for the dependent variables of feeding, resting, locomotion, maintenance and vigilance of family band zebra to assess whether the independent variables of time period, season, sex, age, foal presence, body condition or group size had an effect on their daylight time budgets; with unique zebra identity as random effect on the model intercept. Similar models were fitted for bachelor band members, except that sex and foal presence were not considered as factors influencing their behaviour. We did not fit models to all-occurrence social behaviour because of the relatively small sample sizes.

Data were analysed using the Imer package of R version 3.2.5 (The R Foundation for Statistical Computing, 2011) as well as Statistica version 13.2 (Dell Software, 2016) and Excel 2007 (Microsoft Office, 2007) to calculate descriptive statistics and to obtain mixed-effects repeated measure model estimates. In the mixed models, compound symmetry was used to model possible correlated observations.

5.4 Results

Behavioural data arose from a total of 4048 zebra minutes (total band observation minutes times the number of focal animals in each band for each session) collected during 51 sessions from 162 individual zebra in family bands and 72 individual zebra in bachelor bands. Each individual zebra was sampled 1 – 10 times in family bands and 1-6 times in bachelor bands over the course of the study. All individuals in family bands and bachelor bands were sampled only once per time period on a given day with the exception of two occurrences where a family band was sampled twice within the same time period and 3 occurrences where a bachelor band was sampled twice within the same time period. Distribution of observation time by categorical variable included a minimum of 400 minutes across all categories in family bands, with observation time among bachelor bands being more variable (Table 5.1).

Table 5.1 The distribution of time budget observation sessions and total observed zebra minutes considered in mixed-effects linear models of time budget behaviours at Majete Wildlife Reserve, Malawi.

	Family Bands		**Bachelor Bands**		**Total**	
	Sessions	**Zebra Minutes**	**Sessions**	**Zebra Minutes**	**Sessions**	**Zebra Minutes**
Season						
Early Wet	5	453	0	0	5	453
Late Wet	11	1215	2	62	13	1277
Early Dry	4	401	16	892	20	1293
Late Dry	8	765	5	260	13	1025
Time Period						
08:00-12:00	16	1544	10	446	26	1990
12:01-16:00	5	644	12	698	17	1342
16:00-20:01	7	646	1	70	8	716
Total	28	2834	23	1214	51	4048

During the behavioural sessions, temperatures ranged between 18°C to 41°C. During the early wet season (December to February) temperatures were recorded between 31°C - 36°C; late wet season (March to May) 18°C - 32°C; early dry season (June to August) 19°C - 30°C, and the late dry season (September to November) 26°C - 41°C. Elevation was recorded between 122 to 229 meters above sea level. During 1.9% of the observational sessions precipitation occurred, 62.7% of the observational sessions had no cloud cover, 13.7% had partly cloudy conditions and 23.5% had cloudy conditions.

5.4.1 *Family band time budgets*

Feeding behaviour occupied the largest percentage (mean = 41.8% ± 2.36 [SE]) of family band daylight time budgets (Figure 5.1). The presence of a foal was a significant factor affecting the feeding of zebra occurring in family bands ($F_{1,69} = 11.25$, $p < 0.001$) (Table 5.2). Females with foals spent 20.0% ± 5.58 more daylight time feeding than females without foals (Figure 5.2). The feeding behaviour of individuals in family bands was also significantly influenced by their age ($F_{2,48} = 6.23$, $p = 0.02$) (Table 5.2); with foals feeding 17.3% ± 6.74 more during the day than adult zebra (Figure 5.3). The most significant predictor of the feeding behaviour of members living in family bands, however, was the change in season ($F_{3,144} = 10.27$, $p < 0.001$) (Table 5.2, Figure 5.4). Family band zebra spent 43.5% ± 15.78 more daylight time feeding during the early wet season than the early dry season (Figure

5.4). Group size, body condition, time period and sex were not-significant predictors of the daylight feeding of family band zebra (Table 5.2).

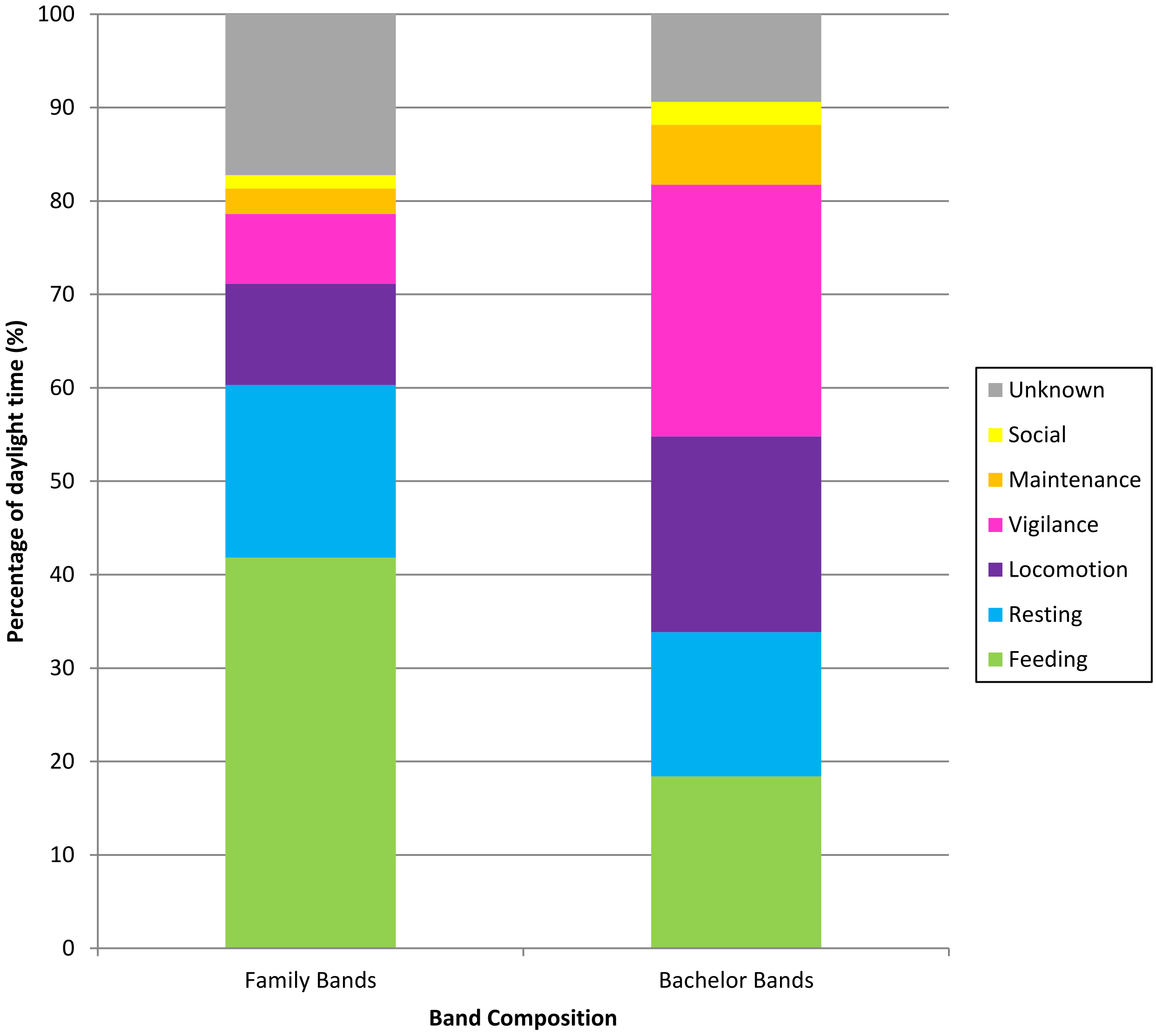

Figure 5.1 Mean allocation of daylight time budget behaviours of family and bachelor band plains zebra (*Equus quagga*) in Majete Wildlife Reserve, Malawi

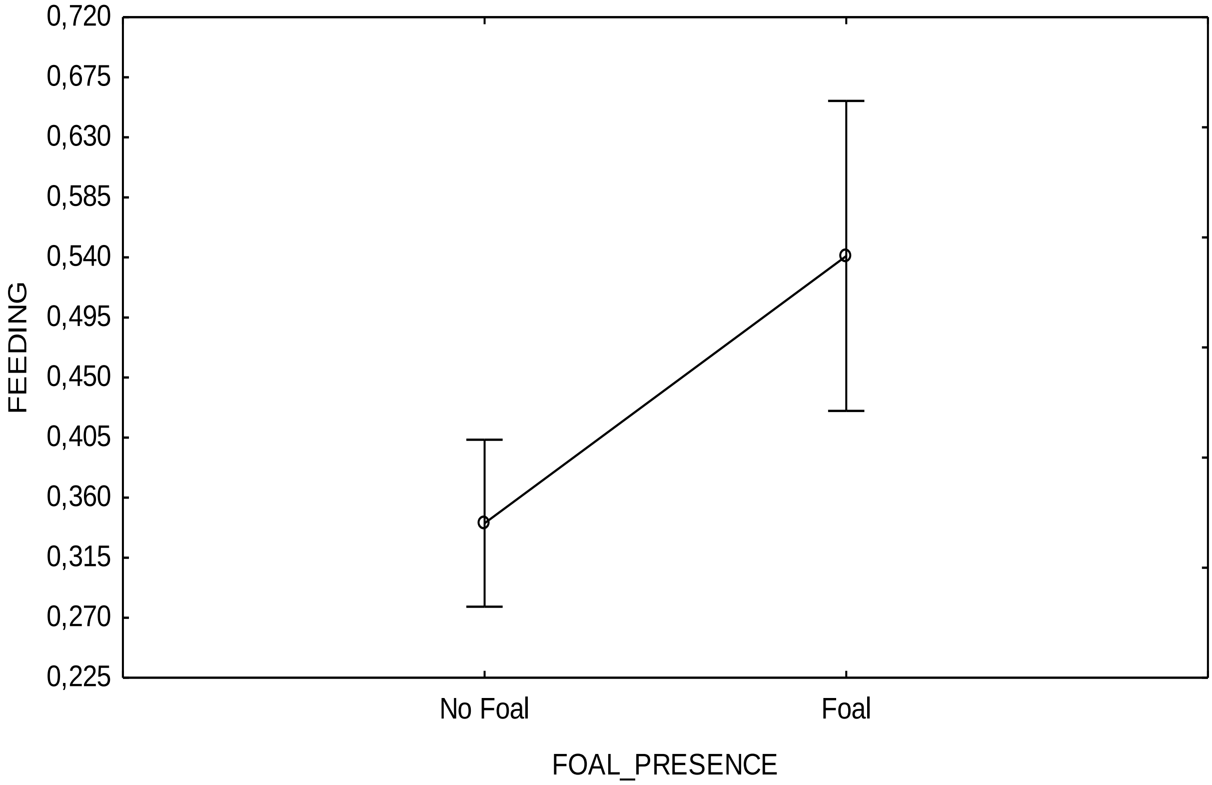

Figure 5.2 Estimated percentage of daylight time spent feeding as a function of foal presence for individual plains zebra in family bands at Majete Wildlife Reserve, Malawi. Error bars depict standard error on each estimate.

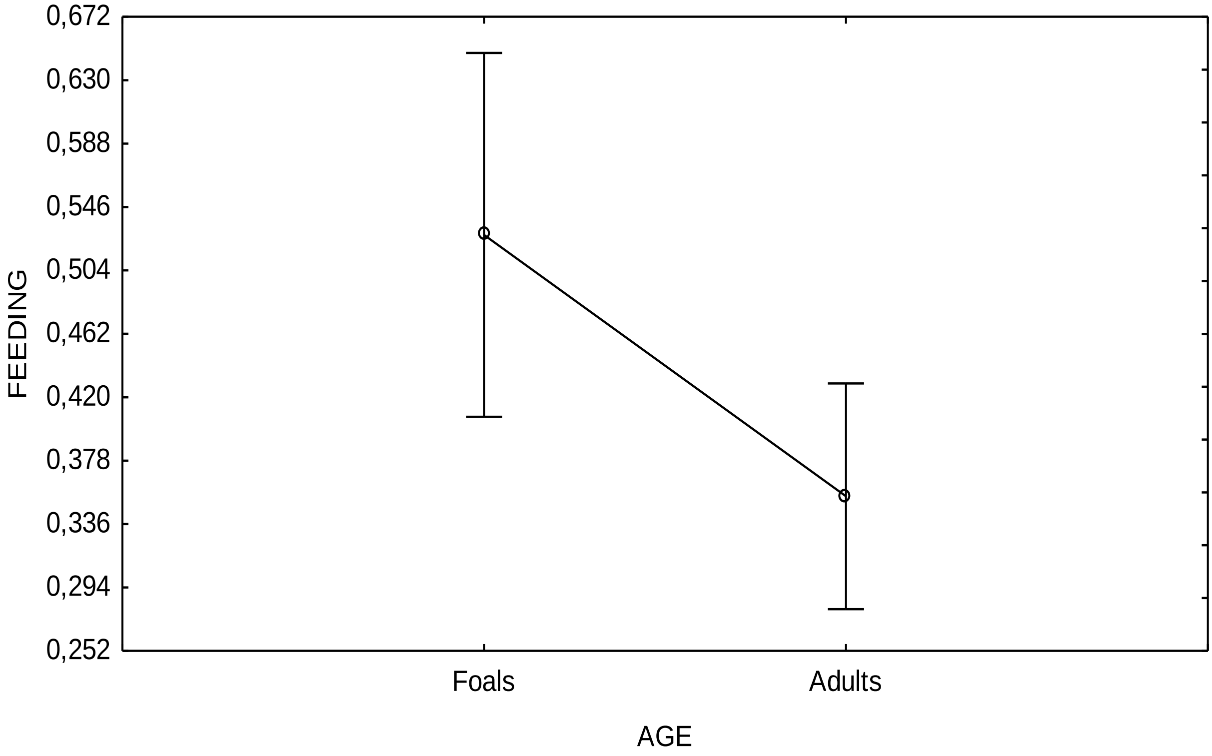

Figure 5.3 Estimated percentage of daylight time spent feeding as a function of age for individual plains zebra in family bands at Majete Wildlife Reserve, Malawi. Error bars depict standard error on each estimate.

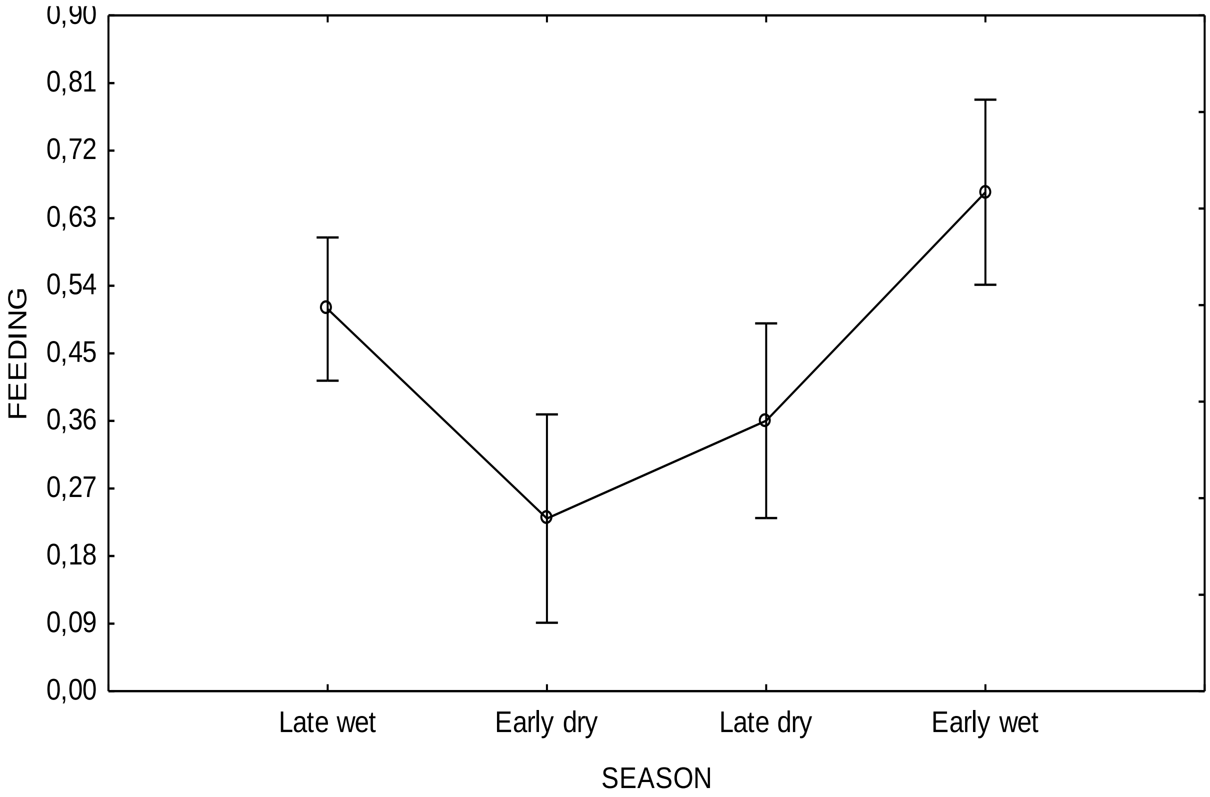

Figure 5.4 Estimated percentage of daylight time spent feeding as a function of season for individual plains zebra in family bands at Majete Wildlife Reserve, Malawi. Error bars depict standard error on each estimate.

Resting behaviour occupied the second largest percentage (18.5% ± 2.21) of family band daylight time budgets (Figure 5.1). The amount of time allocated to resting by family band members was significantly lower during the late wet season compared to the early dry and late dry season ($F_{3,130} = 6.06$, $p < 0.001$) (Figure 5.5). The resting behaviour of family band zebra was not significantly affected by the time period, sex, age, foal presence, body condition or group size (Table 5.2).

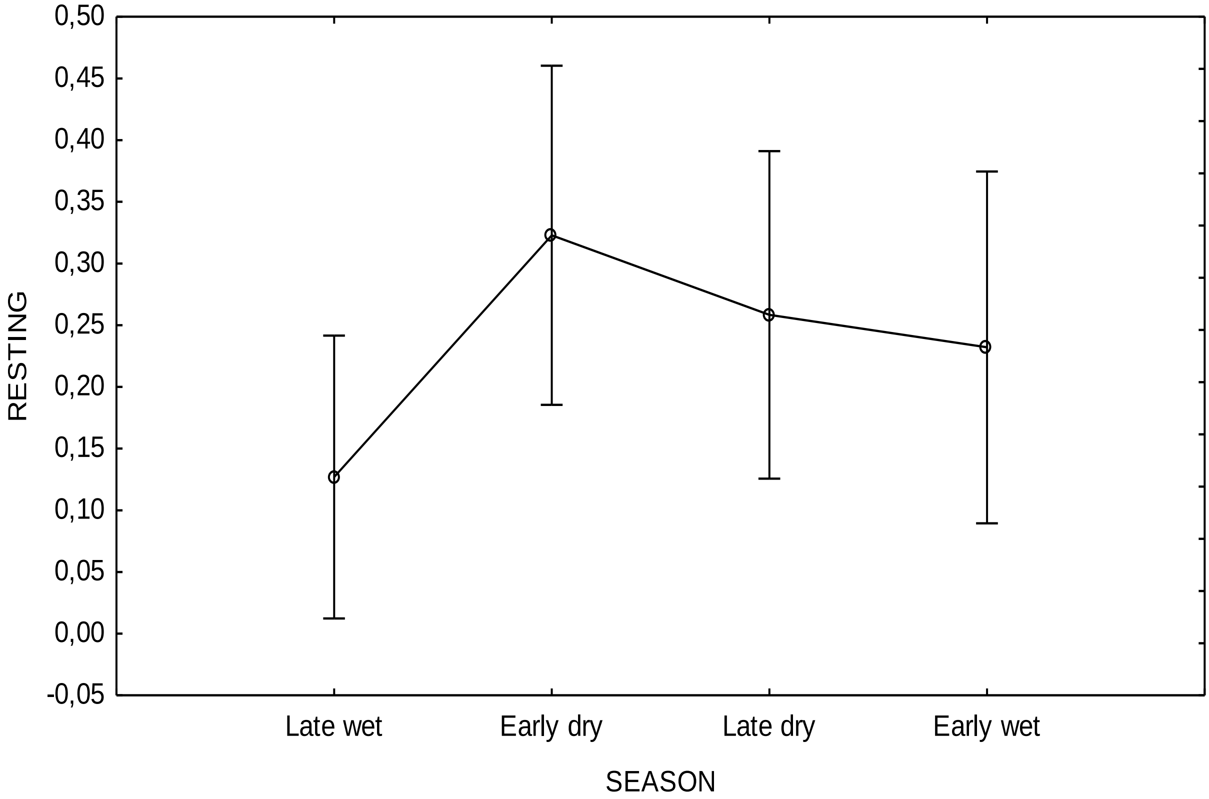

Figure 5.5 Estimated percentage of daylight time spent resting as a function of season for individual plains zebra in family bands at Majete Wildlife Reserve, Malawi. Error bars depict standard error on each estimate.

Thereafter, locomotion behaviour occupied an estimated 10.9% ± 1.05 of family band daylight time budgets (Figure 5.1). The locomotion of zebra occurring in family bands were affected by the season ($F_{3,147}$ = 4.11, p = 0.01) (Table 5.2). Significantly more daylight time (9.6 - 13.4% ± 2.81 - 4.31) was allocated to locomotion during the late dry season compared to the other three seasons (Figure 5.6). Time period, sex, age, foal presence, body condition and group size had no significant effect on the locomotion of family band members (Table 5.2).

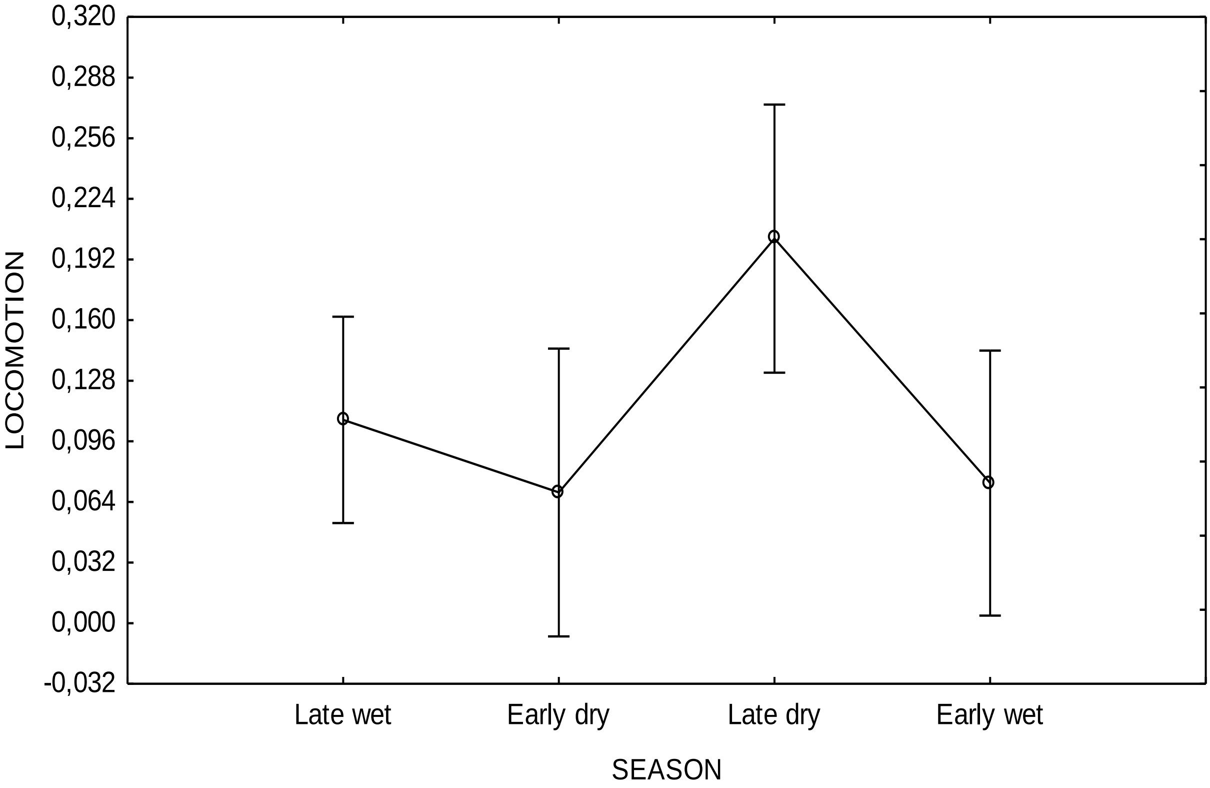

Figure 5.6 Estimated percentage of daylight time allocated to locomotion as a function of season for individual plains zebra in family bands at Majete Wildlife Reserve, Malawi. Error bars depict standard error on each estimate.

Vigilance behaviour occupied an estimated 7.5% ± 0.92 of family band daylight time budgets (Figure 5.1). Age was found to significantly influence the amount of daylight time spent being vigilant by family bands ($F_{1,68} = 5.83$, $p = 0.02$) (Table 5.2), with adults vigilant 8.6% ± 3.50 more than foals during daylight time (Figure 5.7). The vigilance behaviour of family bands was also significantly influenced by the time of day ($F_{2,142} = 3.21$, $p = 0.04$) (Table 5.2), with more time allocated to vigilance during 08:00 to 12:00 than 12:01 to 16:00 or 16:00 to 20:00 (Figure 5.8). Neither season, sex, foal presence, body condition nor group size had a significant influence on the amount of daylight time allocated to vigilance (Table 5.2).

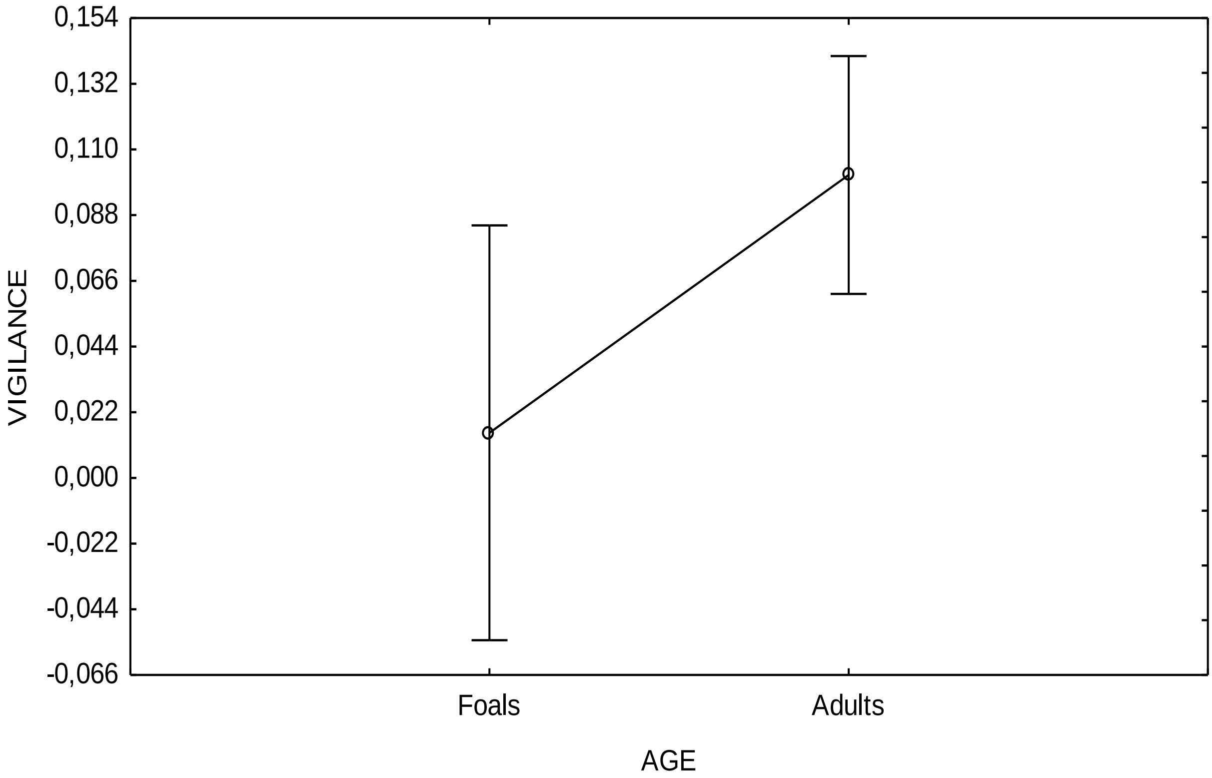

Figure 5.7 Estimated percentage of daylight time allocated to vigilance as a function of age for individual plains zebra in family bands at Majete Wildlife Reserve, Malawi. Error bars depict standard error on each estimate.

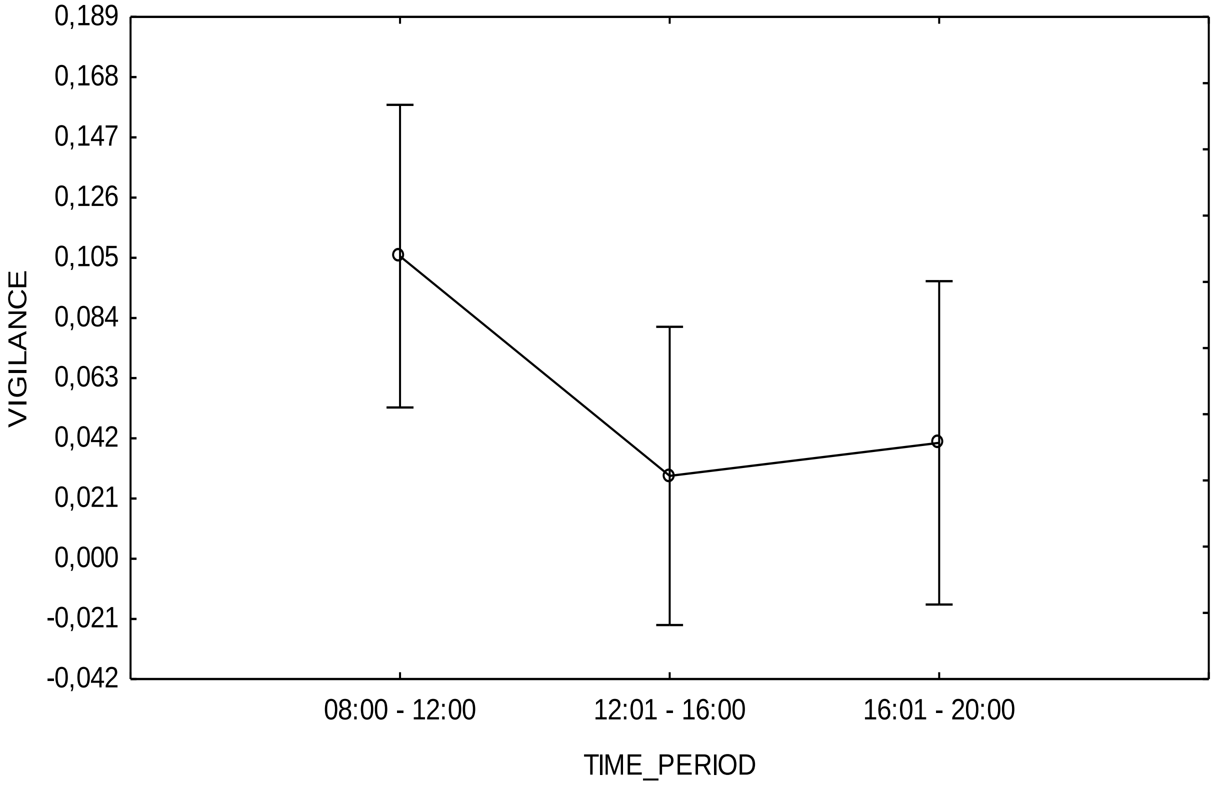

Figure 5.8 Estimated percentage of daylight time allocated to vigilance as a function of time period for individual plains zebra in family bands at Majete Wildlife Reserve, Malawi. Error bars depict standard error on each estimate.

Maintenance occupied a relatively small amount of family band time budgets (2.7% ± 0.92) (Figure 5.1). The amount of daylight time allocated to maintenance for family bands was significantly influenced by the age of the individual ($F_{1,40} = 4.55$, $p = 0.04$) (Table 5.2); with foals spending on average 4.1% more time on maintenance than adult zebra (Figure 5.9). The maintenance behaviour of family bands was not significantly affected by the time period, season, sex, foal presence, body condition or group size (Table 5.2).

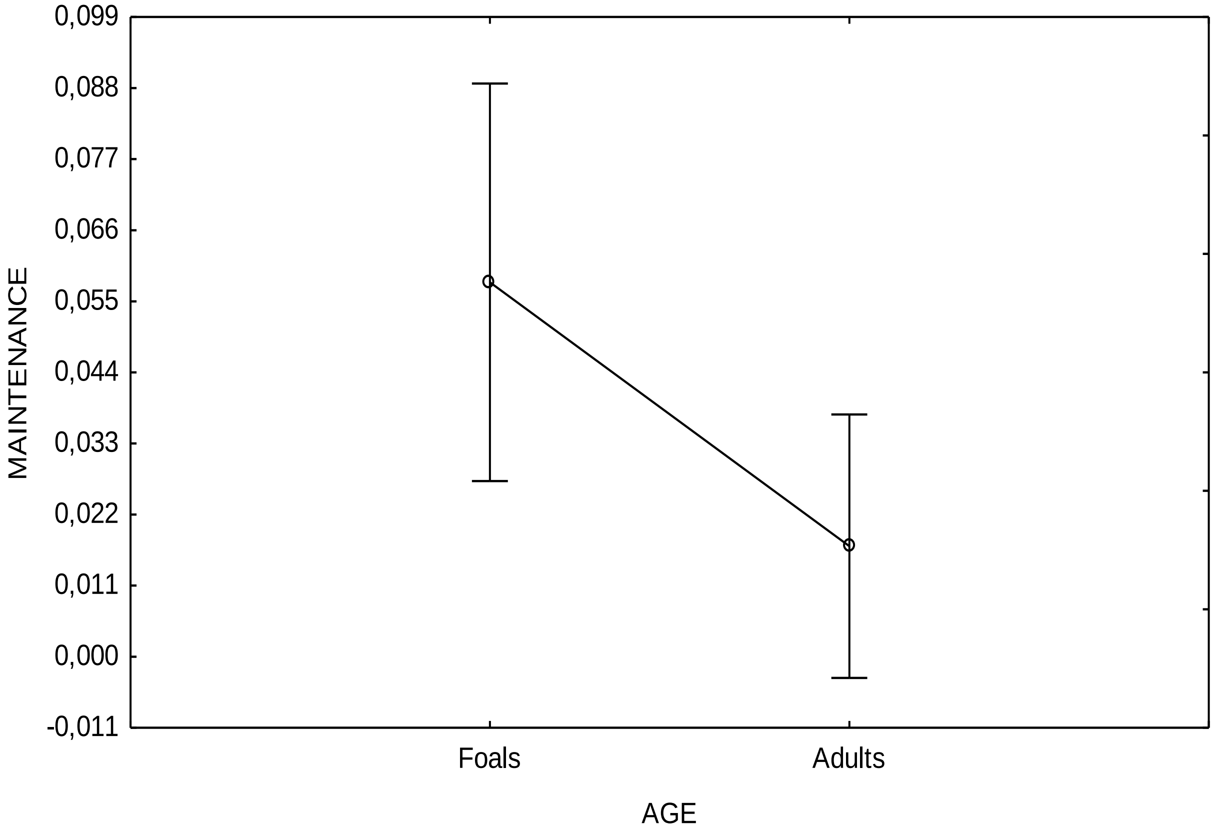

Figure 5.9 Estimated percentage of daylight time allocated to maintenance as a function of age for individual plains zebra in family bands at Majete Wildlife Reserve, Malawi. Error bars depict standard error on each estimate.

Social behaviour occupied the smallest amount of family band daylight time budgets (1.4% ± 0.33) (Figure 5.1). For the remaining 17.3% ± 1.90, family bands were recorded as out of sight or interacting with humans (unknown behaviour) (Figure 5.1).

Table 5.2 Fixed effects estimates in models of time budgets for plains zebra in family bands at Majete Wildlife Reserve, Malawi.

Behaviour	**Effect**	**Estimate ± SE**	**df$_{NUM}$**	**df$_{DENOM}$**	**F**	**p**
Feeding	Age	-0.17 ± 0.07	1	48	6.23	**0.02**
	Body condition	0.00 ± 0.04	1	143	0.02	0.89
	Foal presence	0.20 ± 0.06	1	69	11.25	**0.001**
	Group size	-0.03 ± 0.02	1	55	3.24	0.08
	Season	-0.09 ± 0.07	3	144	10.27	**< 0.001**
	Sex	-0.01 ± 0.07	2	94	0.88	0.42
	Time period	-0.04 ± 0.07	2	144	0.97	0.38
Locomotion	Age	0.05 ± 0.04	1	62	1.69	0.20
	Body condition	0.02 ± 0.02	1	148	0.71	0.40
	Foal presence	0.01 ± 0.03	1	78	0.03	0.87
	Group size	-0.01 ± 0.01	1	70	0.30	0.58
	Season	0.01 ± 0.04	3	146	4.11	**0.01**
	Sex	0.03 ± 0.04	2	108	2.56	0.08
	Time period	0.05 ± 0.04	2	142	2.51	0.08
Maintenance	Age	-0.04 ± 0.02	1	40	4.55	**0.04**
	Body condition	0.01 ± 0.01	1	136	0.54	0.46
	Foal presence	0.01 ± 0.02	1	64	0.69	0.41
	Group size	-0.01 ± 0.00	1	44	2.86	0.10
	Season	-0.02 ± 0.02	3	143	0.68	0.57
	Sex	-0.02 ± 0.02	2	83	0.93	0.40
	Time period	0.02 ± 0.02	2	145	0.60	0.55
Resting	Age	-0.02 ± 0.08	1	139	0.04	0.84

	Body condition	-0.02 ± 0.03	1	138	0.32	0.58
	Foal presence	-0.05 ± 0.07	1	131	0.59	0.45
	Group size	0.01 ± 0.02	1	95	0.06	0.81
	Season	0.14 ± 0.06	3	130	6.06	**0.001**
	Sex	0.01 ± 0.07	2	138	0.19	0.83
	Time period	-0.11 ± 0.06	2	129	2.32	0.10
Vigilant	Age	0.09 ± 0.04	1	68	5.83	**0.02**
	Body condition	0.01 ± 0.02	1	148	0.14	0.70
	Foal presence	-0.05 ± 0.03	1	81	2.77	0.10
	Group size	0.00 ± 0.01	1	74	0.00	0.96
	Season	0.01 ± 0.03	3	146	2.30	0.08
	Sex	0.00 ± 0.03	2	111	0.82	0.44
	Time period	-0.07 ± 0.03	2	141	3.21	**0.04**

5.4.2 *Bachelor band time budgets*

Bachelors spent the majority of their time being vigilant (27.0% ± 2.72) (Figure 5.1). The time bachelors allocated to vigilance was influenced by both the time period ($F_{2,64} = 8.01$, $p < 0.001$) and season ($F_{2,64} = 4.14$, $p = 0.02$) (Table 5.3). Bachelors allocated significantly more time to vigilance behaviour between 16:01 to 20:00 than either 08:00 to 12:00 (30.6% ± 10.50) or 12:01 to 16:00 (43.1% ± 10.99) (Figure 5.10). They also spent significantly more time being vigilant during the early dry (29.8% ± 10.34) and late dry season (29.4% ± 14.56) compared to the late wet season (Figure 5.11). Body condition and group size however had no significant effect on the vigilance behaviour of zebra in bachelor bands (Table 5.3)

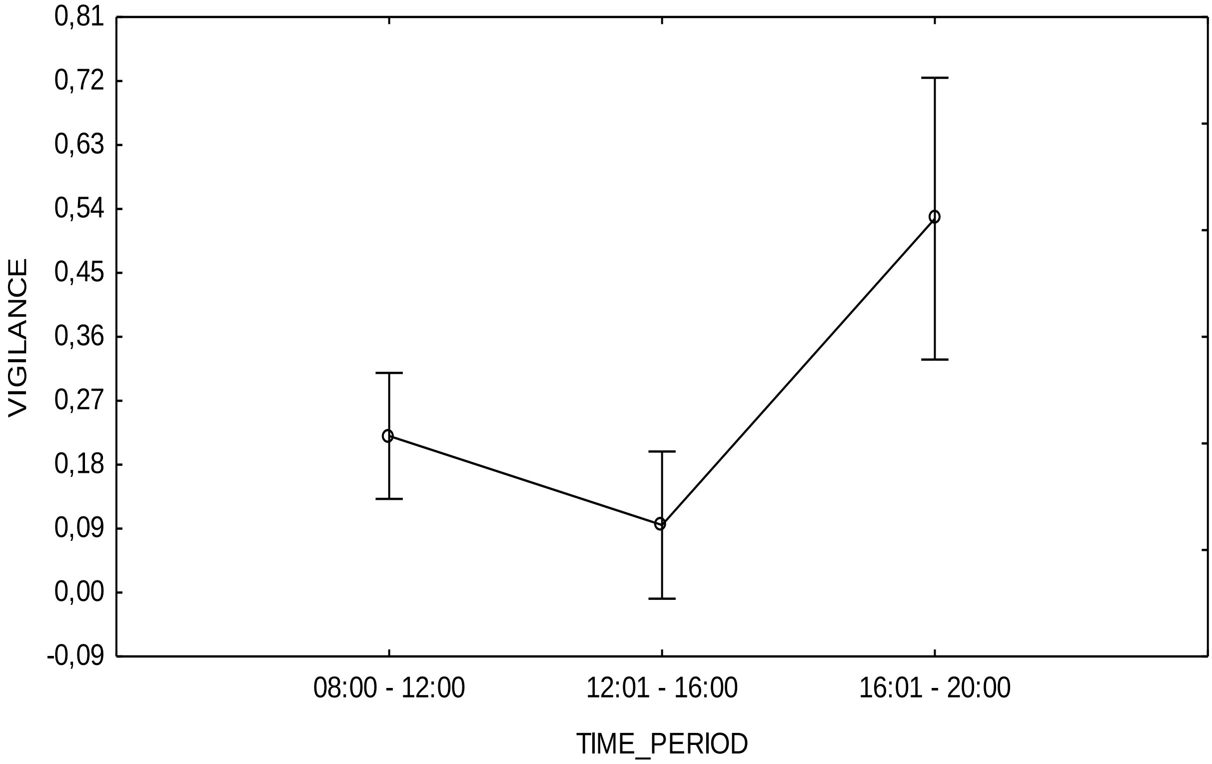

Figure 5.10 Estimated percentage of daylight time allocated to vigilance as a function of time for individual plains zebra in bachelor bands at Majete Wildlife Reserve, Malawi. Error bars depict standard error on each estimate.

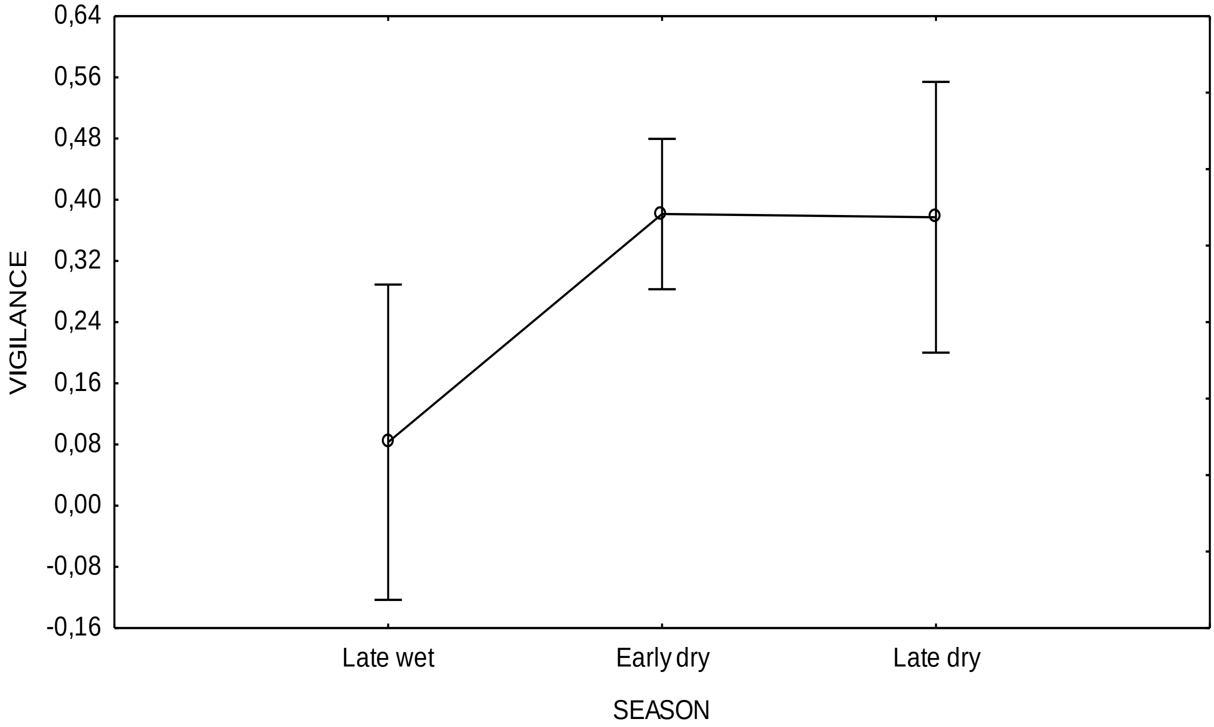

Figure 5.11 Estimated percentage of daylight time allocated to vigilance as a function of season for individual plains zebra in bachelor bands at Majete Wildife Reserve, Malawi. Error bars depict standard error on each estimate.

Locomotion behaviour also occupied a relatively large percentage of bachelor band daylight time budgets (21.0% ± 2.05), followed by feeding which occupied an estimated 18.4% ± 2.32 (Figure 5.1). Neither locomotion nor feeding behaviour of bachelor bands was influenced by body condition, group size, season or time period (Table 5.3).

Resting behaviour occupied an estimated 15.4% ± 2.85 (Figure 5.1) of bachelor zebra daylight time budgets and was significantly influenced by the body condition of bachelors ($F_{1,64} = 5.28$, $p = 0.03$) (Table 5.3). As body condition improved, the time allocated to resting decreased with a total of 25.8% ± 11.04 (Figure 5.12). Resting behaviour of bachelors bands was not affected by either group size, season or time period (Table 5.3)

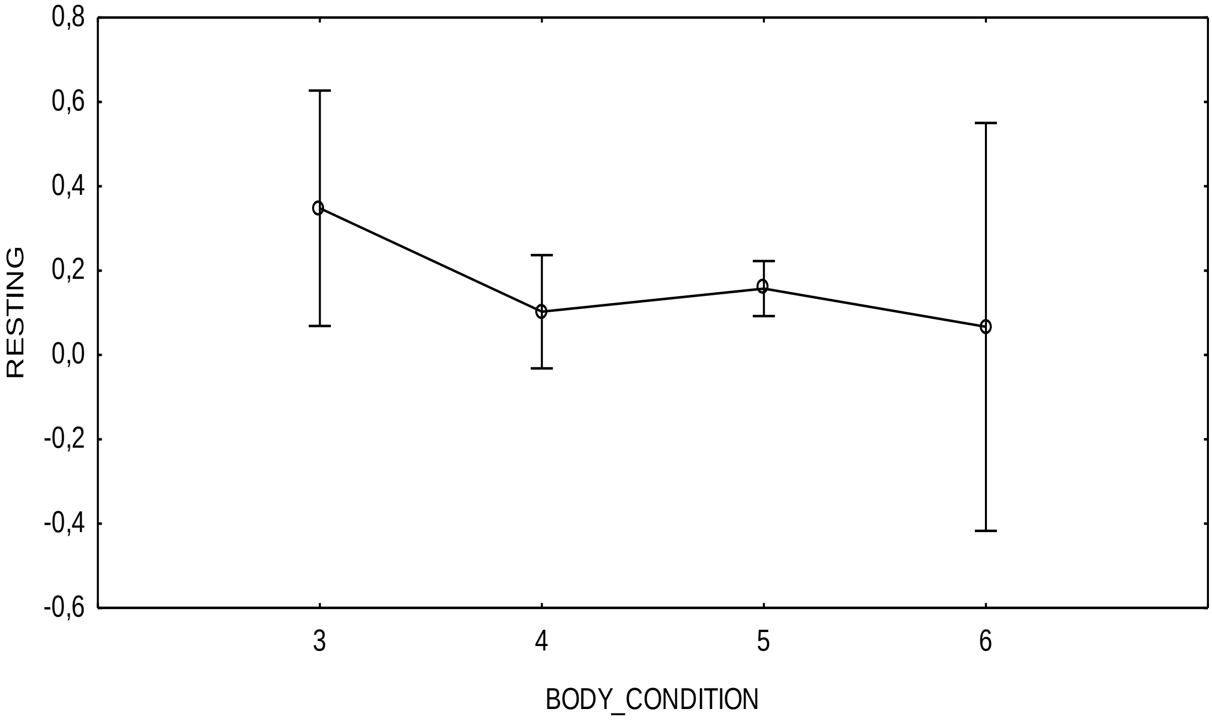

Figure 5.12 Estimated percentage of daylight time spent resting as a function of body condition for individual plains zebra in bachelor bands at Majete Wildlife Reserve, Malawi. Error bars depict standard error on each estimate.

A relatively small amount of bachelor zebra daylight time budgets was allocated to maintenance behaviour (6.4% ± 1.86). The maintenance behaviour of bachelor bands was not significantly influenced by body condition, group size, season or time period (Table 5.3). Social behaviour occupied the smallest amount of bachelor band daylight time budgets (2.4% ± 0.68) (Figure 5.1). The remaining 9.7% ± 1.74 of bachelor band time budgets were recorded as out of sight or interacting with humans (unknown behaviour) (Figure 5.1).

Table 5.3 Fixed effects estimates in models of time budgets for plains zebra in bachelor bands at Majete Wildlife Reserve, Malawi.

Behaviour	**Effect**	**Estimate ± SE**	**df$_{NUM}$**	**df$_{DENOM}$**	**F**	**p**
Feeding	Body condition	0.05 ± 0.09	1	65	0.25	0.62
	Group size	-0.01 ± 0.03	1	64	0.06	0.82
	Season	-0.06 ± 0.11	2	64	0.01	0.99
	Time period	0.01 ± 0.13	2	64	3.06	0.05
Locomotion	Body condition	0.14 ± 0.09	1	64	2.60	0.11
	Group size	-0.01 ± 0.02	1	57	0.17	0.68
	Season	0.13 ± 0.12	2	62	0.83	0.44
	Time period	-0.05 ± 0.09	2	59	0.38	0.69
Maintenance	Body condition	0.02 ± 0.07	1	64	0.11	0.74
	Group size	0.01 ± 0.02	1	48	0.44	0.51
	Season	-0.02 ± 0.09	2	58	0.03	0.97
	Time period	0.02 ± 0.07	2	51	0.57	0.57
Resting	Body condition	-0.26 ± 0.11	1	64	5.28	**0.03**
	Group size	-0.03 ± 0.03	1	65	0.73	0.40
	Season	-0.27 ± 0.15	2	63	2.24	0.12
	Time period	0.15 ± 0.13	2	64	0.81	0.45
Vigilant	Body condition	-0.02 ± 0.09	1	65	0.05	0.83
	Group size	-0.03 ± 0.03	1	64	1.36	0.25
	Season	0.30 ± 0.12	2	62	4.139	**0.02**
	Time period	-0.37 ± 0.11	1	64	8.011	**< 0.001**

5.4.3 *Social behaviour*

Social behaviours such as mutual grooming and non-agonistic social behaviour (including pair-bonding, olfactory investigation, nudging, play, urine and faecal marking, and sniffing of other band members' urine and faeces) were the most commonly observed behaviours exhibited between individuals (Table 5.4). Individuals within bachelor bands were never observed mutual grooming, but engaged in other forms of non-agonistic social behaviour 6.1 times per hour. Mutual grooming in family bands made up 22.9% of all non-agonistic social behaviours (excluding herding). Non-agonistic social behaviours were observed at a rate of 2.3 times per hour in family bands (including mutual grooming). Herding behaviour from a band stallion toward other members of the band was observed at a rate of 0.5 times per hour.

Of the 41 agonistic events detected within bachelor bands, 36.6% were threats and 43.9% were kicks, stomps or bites, with the remaining percent comprised of pushing, chasing, and rearing (Table 5.4). Agonism within family bands exhibited the same pattern but with less frequency: of 21 agonistic events detected, 38.1% were threats and 42.9% were kicks, stomps, or bites (Table 5.4). Agonism was observed 1.8 times per hour in bachelor bands as compared to 0.5 times per hour in family bands.

Table 5.4 Observed social behaviour events for family and bachelor bands of plains zebra (*Equus quagga*) in Majete Wildlife Reserve, Malawi

	Behaviour	**Bachelor**		**Family**	
		Count	**Rate**	**Count**	**Rate**
Agonistic					
	Threats	15	0.7	8	0.2
	Bumps and pushing	4	0.2	1	0.0
	Chases	2	0.1	3	0.1
	Kick, bites, and stomping	18	0.8	9	0.2
	Rearing	2	0.1	0	0.0
Affiliative					
	Herding	0	0.0	23	0.5
	Non-agonistic social	140	6.1	81	1.8
	Mutual grooming	0	0.0	24	0.5
	Submission	1	0.0	0	0.0

5.5 Discussion

5.5.1 *Time budgets*

In MWR family bands allocated the majority of their daylight time budgets to feeding behaviour (41.8% of their daylight time budgets). In comparison, a previous study conducted by Neuhaus and Ruckstuhl (2002) on the daylight time budgets of plains zebra in Etosha National Park, Namibia, indicated that zebra spend the majority of their time grazing (54.3%). Five other studies conducted in Lake Manyara National Park, Ngorongoro Conservation Area and Serengeti National Park, Tanzania, as well as Amboseli National Park and Samburu-Buffalo Springs Game Reserves, Kenya, and Moolmanshoek Private Game Reserve, South Africa, indicated that zebra spend 60 - 70% of their time grazing (Beekman & Prins, 1989; Gakahu, 1984; Grogan, 1978; Rubenstein, 1994; Simpson *et al.*, 2012). Across studies, plains zebra spend roughly half of their time feeding. While it is possible that zebra at MWR distributed their time differently during nocturnal hours when we did not collect data, remote cameras aimed at waterholes over the same time period as this study did suggest that these zebra exhibited more limited activity during the night (17% of detections were nocturnal during the wet season and 31% were nocturnal during the dry season: see Chapter 4). The potential differences estimated between the amount of daylight time allocated to feeding between zebra in MWR compared to the rest of Africa may be due to inequities in study design, may be indicative of greater nocturnal activity at MWR, or may reflect an actual difference in nutrient and energy requirements, the rate at which food can be ingested or the quality and abundance of digestible food (Beekman & Prins, 1989).

When investigating the seasonal variation in the feeding behaviour of family bands in MWR, it appears that the somewhat smaller amount of time allocated to feeding might more specifically reflect a lack of resources during the dry season. Previous studies have found that in order for zebra and other equids to meet their energy requirements, 60% of their time needs to be allocated towards grazing under optimal conditions and 80% under poor conditions (Bell, 1971; Blom, 2009; Rubenstein, 1994; Tyler, 1972). In MWR, during the wet season when food is abundant and high in quality, family bands graze for 50.9 - 66.5% of the time compared to 23.0 - 36.0% of the time during the dry season when grazing conditions are not optimal. This decrease in the amount of time allocate to feeding during the dry season, instead of an increase as displayed by other study suggest that the availability of resources are limiting in MWR; for if only the quality of the food decreased and not the quantity, zebra would have displayed an increase in the amount of time allocated to feeding during the dry season instead of a decrease. The significant seasonal variation in the amount of time family bands allocate towards feeding in MWR confirms that the temporal and spatial abundance of resources shape the feeding behaviour of zebra (Rubenstein, 2010). It may be of concern for zebra in MWR if animals are unable to compensate for reduced food quality in the dry season by increasing their grazing time due to a lack of resources (Beekman & Prins, 1989). The results therefore suggest that MWR may not adequately include both summer and winter feeding areas (Penzhorn & Novellie, 1991). In order to aid the conservation of zebra in MWR, the expansion of the reserve to include winter feeding habitats may be needed or feeding may need to be supplemented during extremely dry years or after extreme fires to prevent zebra mortalities.

Apart from season acting as a significant predictor of the feeding behaviour of family bands, age and foal presence also influenced their feeding. Foals were observed feeding 17.3% more than adult zebra in family bands. The difference in the amount of time foals allocated to feeding compared to adults can be as a result of foals trying to meet the added energy demands of growing (Blom, 2009). In addition, females with foals graze 20.0% more than individuals without foals. Other studies conducted on equids also observed lactating females spending more time grazing than non-lactating females (Boyd, 1988; Duncan, 1985; Neuhaus & Ruckstuhl, 2002). It is proposed that females that are experiencing the added cost of producing milk for their foals (approximately 11 - 16 months until foals are weaned) are forced to behave differently in order to meet their energetic requirements (Nuñez, Asa & Rubenstein, 2011; Rubenstein, 1994; Smuts, 1976). Conclusively, age and reproductive state influences the energy requirements of family bands and in turn can result in a variation in time budgets (Halle & Stenseth, 1997).

In contrast to family bands who allocate 41.8% of their daylight time budgets to feeding, bachelor bands in MWR only appear to have fed 18.4% of the time. The largest proportion of bachelor band daylight time budgets was however allocated towards vigilance (26.9%). This corresponds to the findings of other studies in which bachelors were observed to generally graze 20 - 30% less than family members, as males spend less time feeding and more time being vigilant (Rubenstein, 1994; Simpson *et al.*, 2012). The variation in the amount of time allocated towards feeding and vigilance between bachelor and family bands may thus be due to a variation in band composition. Bachelors generally occurred in smaller groups than family band zebra in MWR and therefore possibly have to allocate more daylight time to vigilance behaviour in order to reduce their predation risk (Chapter Two; Rubenstein, 2010). Another possibility is that bachelor bands have less energy requirements than family band members, especially compared to females (since they do not have to care for a foetus or produce milk) and are therefore able to spend less time foraging and more time being vigilant (Clutton-Brock, 1991, Simpson *et al.*, 2012). It is also possible that variation in the amount of time allocated to vigilance and feeding between family and bachelor bands may be due to observation bias, since bachelors may have been feeding in areas that were not accessible to observers.

The results from this study also suggest that both time period and season significantly affected the vigilance behaviour of bachelors, with time period being the more significant predictor. The vigilance behaviour of family bands was influenced by both time period and age, with age being the more significant predictor. On average adult zebra in MWR allocated an estimated 8.6% more time to vigilance behaviour than foals, indicating that it is the responsibility of the adult members of a family band to keep an eye out for predators and to protect their offspring from danger (King *et al.*, 2016). This can possibly also explain why foals spend more time on maintenance behaviour than adults. Since foals spend less time on vigilance behaviour, they are able to conversely spend more time on maintenance behaviour (especially grooming, object play and play fighting). It is of importance that foals are able to spend more time on maintenance behaviour as it develops their motor skills and fighting expertise (Cameron, Linklater, Stafford & Minot, 2008; Khalil & Kaseda, 1998; Waring, 1983). It has also been noted that individuals who allocate more time to these types of behaviours improve their chance at survival by either improving their condition as a yearling or through the experiences learned through object play and play fighting (Cameron *et al.*, 2008; King *et al*,. 2016).

Family bands were significantly more vigilant in the morning (08:00 - 12:00) than any other time period (similar results were found in a study conducted by Simpson *et al.*, 2012) and bachelors were significantly more vigilant in the afternoon (16:01 - 20:00). The difference in the time of day family and bachelor bands allocate more time to being vigilant can be due to the unequal distribution of sampling efforts across the different time periods for family and bachelor bands. However, the amount of time allocated to being vigilant by both family and bachelor bands were the lowest during midday (12:01 - 16:00). These results suggest that zebra decrease the amount of time allocated to vigilance behaviour when predation is less likely, since predators are generally inactive during midday (Hayward & Slotow, 2009). The amount of time bachelors allocate to being vigilant was also significantly higher during the dry season than the wet season. This is likely due to the increased risk of being detected by predators in the dry season when compared to the wet season, due to the limited amount of vegetation cover during the dry season in MWR (Thaker, Vanak, Owen, Ogden & Slotow, 2010). Predation thus likely shapes the vigilance behaviour of zebra at MWR.

Results indicate that locomotion behaviour of family bands in MWR was affected by season. This is in agreement with a study conducted on Cape mountain zebra (*Equus zebra zebra*) which observed a seasonal variation in their locomotion behaviour (Penzhorn & Novellie, 1991). The authors suggested that movement of Cape mountain zebra was associated with a relative change in diet quality, as well as thermoregulatory behaviour. They observed that when climatic conditions were unfavourable (with rainfall acting as a stronger driver than temperature), the Cape mountain zebra allocated more time to locomotion in order to seek shelter. However in MWR, the amount of daylight time allocated to locomotion was significantly more in the late dry season (when rainfall was absent or limited) than any other time of the year. This suggests that the increase in daylight time allocated to locomotion in the late dry season in MWR is most likely a result of the seasonal variation of resources. This is in agreement with other studies conducted on equids that have also concluded that the amount of time spent moving is associated with a change in resources over seasons, since the relative distance between water sources and prime feeding areas increases during drier months (Berman, 1991; Brooks, 2005; Hampson, de Laat, Mills & Pollitt, 2010; King *et al*., 2016).

Season influenced resting behaviour of family bands in MWR, with more time allocated to resting during the dry season (winter) than the late wet season (summer). This is in contrast to previous findings, as equids generally spend less time resting in the winter than in the summer (Keiper *et al.,* 1980). This is possibly as a consequence of the limited food resources during the dry season in MWR resulting in a decrease in the amount of time allocated to feeding during this time of the year (as previously discussed) and conversely resting time increases. It is common that resting behaviour increases when feeding decreases, because of compositional trade-offs (King *et al.*, 2016). Given the increase in nocturnal detections on our waterhole cameras during the dry season (Chapter 4), it is likely that zebra are also compensating in part by becoming more active at night.

Group size did not affect the behaviour of zebra in MWR. Typically for herbivores an increase in group size will result in an increase in the amount of time allocated to feeding, since less time is allocated to vigilance behaviour as the risk of predation decreases (Ransom *et al.*, 2010). However, an increase in group size can possibly also result in increased competition for feeding (Rubenstein, 1994). Zebra are extremely tolerant of one another due to the benefits of group living and this possibly allows for a peaceful co-existence irrespective of group size (Rubenstein, 1994). Sex also had no effect on zebra behaviour. This corresponds to the findings of studies conducted on both zebra and feral horses (Duncan, 1992; Neuhaus & Ruckstuhl, 2002). It is hypothesized that to ensure the stability of family bands, synchronization of behaviour between different sexes within a family band should be high (Neuhaus & Ruckstuhl, 2002). The similarity in body mass between males (250kg) and females (220kg) may be a prerequisite to allow for the synchronization of behaviour between different sexes (Estes, 1991; Owen-Smith, 1988, Ruckstuhl & Neuhaus, 2000). A variation in the body mass between sexes generally results in different energy requirements for females and males, which in turn leads to a sexual variation in time budgets (Neuhaus & Ruckstuhl, 2002).

5.5.2 *Social behaviour*

In comparison to other studies conducted on equids, rates of non-agonistic social behaviour for zebra in MWR were high. Family bands displayed 2.3 acts/hour and bachelor bands, 6.1 acts/hour, compared to Grevy's zebra (*Equus grevyii*), 0.47 acts/hour; feral ass (*Equus africanus*), 0.3 acts/hour; Przewalski's horse (*Equus ferus przewalskii*), 0.04 - 0.22 acts/hour; and free-living domestic horse (*Equus ferus caballus*), 0.004 - 0.24 acts/hour (Heitor, do Mar Oom & Vicente, 2006; King, 2002; Moehlman, 1998; Mooring, Benjamin, Harte & Herzog, 2000; Sigurjónsdóttir, van Dierendonck, Snorrason & Thorhallsdóttir, 2003). The possible explanation for the higher rates of non-agonistic social behaviour compared to other equid populations is that zebra in MWR need to relieve more stress between individuals, as it is argued that non-agonistic social behaviours have evolved to sooth members partaking in the act (King *et al*., 2016). Their high stress levels can be due to the recent presence of predators, the lack of resources during the dry season or as a consequence of their reintroduction to the reserve. However, such conclusions can only be made after comparing the non-agonistic rates of Majete's zebra to other plains zebra populations because the higher non-agonistic rates observed might be a consequence of species-specific behaviour of plains zebra – to our knowledge these data are not available.

Mutual grooming made up 22.1% of all non-agonistic social behaviour (excluding herding) in family bands; whereas mutual grooming was never observed among individuals in bachelor bands. Mutual grooming occurs when two individuals scratch or pluck one another's coat with their teeth while standing in reverse parallel (Feh and de Mazières, 1993). Mutual grooming is considered important for family bands because it reinforces bonds between individuals, reduces aggression by decreasing their heart rates and by soothing each of the individuals partaking in the act (Andersen, 1992; Crowell-Davis, Houpt & Carini, 1986; Feh & de Mazières, 1993; Feist & McCullough, 1976; Kimura, 2000). The stable bonds of family groups (as discussed in Chapter Two) is therefore partially maintained by mutual grooming. It can also decrease conflict associated with weaning and enhance reproductive success with the establishment of stable female-female and female-male relationships (Cameron, Setsaas & Linklater, 2009; Keiper, 1988; Linklater, Cameron, Minot & Stafford, 1999; Penzhorn, 1984). By enhancing the stability of family bands with the aid of mutual grooming, family bands are able to increase their ability as a group to protect their foals against danger, as zebra rely on each other for the successful rearing of young (Simpson *et al*., 2012).

The fact that no mutual grooming was observed among members of bachelor bands is surprising, as mutual grooming also has the added benefit of removing parasites and loose hair from hard to reach places that can otherwise only be maintained by rolling (King *et al*., 2016; Tyler, 1972). Mutual grooming evolved to maintain family-type bonds and thus may not be a prevalent behaviour among all-male groups (King *et al*., 2016). The lack of mutual grooming events and the unstable bonds of bachelor bands (as discussed in Chapter Two) might also possibly explain why bachelor bands had a higher agonism rate than family bands.

Compared to other equid populations, the agonistic rates observed in MWR where in line with other studies: 1.8 acts/hour for bachelor bands, and 0.5 acts/hour for family bands compared to 0.01 - 3.50 acts/hour observed for feral horse and 0.35 acts/hour observed for Przewalski's horse (King, 2002; Ransom *et al*., 2010; Wells & von Goldschmidt-Rothschild, 1979). Furthermore, the results suggest that for wild plains zebra, agonistic behaviour is very rare and seldom results in highly agonistic expressions, as striking and boxing were never observed during this study (King *et al*., 2016).

5.6 Conclusion

The findings from this study suggest that the environment (especially resource availability) and energy requirements are the central determinants influencing the time budgets of zebra. The study also suggests that the mutual grooming among individuals signifies the thread that holds family bands together. The outcome from this study may assist with the future conservation of zebra, especially with regards to a costly modification of their time budget activities and social interactions and may consequently lead to better management of zebra in order to sustain healthy populations.

Even though this study has provided a foundation for understanding wild zebra time budgets and social behaviour at MWR, future studies can be conducted in order to provide a greater in-depth analysis. Recommendations for future studies are as follow:

1) Daylight time budgets should be lengthened to 24-hour observations, in order to investigate how zebra allocate their time over an entire day. This will also allow researchers to confirm if a decrease in the amount of daylight time allocated to feeding during the dry season is because they allocate more time to feeding at night during this particular season; or if feeding remains low throughout 24-hours due to the poor quality of grass during the dry season. In addition to a 24-hour time budget analysis, a vegetation analysis should also be conducted to ground truth and assess the extent of decline in the quality and abundance of grass within MWR as the season's progress from wet to dry.

2) It has been suggested that predators will affect the time budgets of equids, especially with regards to the time of day at which equids conduct their activity (Blom, 2009; Simpson *et al*., 2012). However, few empirical data are available on how predators affect the time budgets of equids (King *et al*., 2016). Due to the relatively small predator population currently within the reserve (as discussed in Chapter Two), the daylight time budgets for zebra which occur with predators at relatively low densities has been established during this study. If this study is continued as the predator population increases within the reserve, then it would be possible to quantify the effect predators occurring at relatively high densities will have on the daylight time budgets of zebra within MWR.

3) The time budgets of zebra during drought-stricken years can be investigated and compared to the time budgets of zebra during favourable climatic years to better understand how the time budgets of zebra will be affected by climate change.

4) It can also prove useful to conduct time budget studies on zebra pre-reintroduction and post-reintroduction, in order to quantify how reintroductions may alter the behaviour of zebra; as well as how long it will take zebra to display similar time budgets to those prior to reintroduction. The comparison of time budgets pre- and post-reintroduction can also allow researchers to establish how zebra adjust their time allocation to cope with the exposure of new environmental conditions. For example in MWR this would have been useful to establish how the inherently poor quality of miombo savanna woodlands have affected the time budgets of zebra previously occurring in other vegetation types of better quality.

5) It has been observed that individuals who spend more time on maintenance behaviour, object play and play fighting, as foals and yearlings, improve their chances at survival by improving their condition, motor skills and fighting expertise (Cameron *et al*., 2008; King *et al*., 2016). However, few studies have aimed to quantify how much time foals and yearlings should dedicate to these particular behaviours in order to enhance their survival.

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Chapter Six

Research findings, conclusions and management recommendations

6.1 Overview

The fragmentation of ecosystems, due to the increasing human population and change in climate has resulted in many plains zebra populations declining or becoming permanently isolated. Successful conservation efforts are now relying on reintroductions to recover wildlife or build connectivity between populations. This study aimed to determine the demographics, diet, artificial waterhole usage and behaviour of plains zebra in Majete Widlife Reserve (MWR) more than ten years after their initial reintroduction. The findings from this study have provided a foundation to understanding the ecology of MWR's plains zebra and will assist with the development of a feasible and effective Conservation and Management Plan in order to manage their population. A summary of the key research findings and their implications for management are discussed in detail.

6.2 Research findings

Chapter Two: Demography and social organization of reintroduced plains zebra

- A total of 571 individual plains zebra were counted in the most recent aerial survey (September 2015), of which the current study was able to formally indentify 243 individual plains zebra using photographs to determine individual stripe patterns.
- By December 2017 plains zebra were found to have dispersed throughout the entire reserve, with densities increasing along a west to east gradient.
- The population structure of the sample population was found to be 69.1% adults (>24 months), 13.2% yearlings (12 - 24 months) and 17.7% foals (<12 months). The adult plains zebra sex ratio in MWR was 0.8:1.0 (male:female) and the sex ratio for yearlings and foals remains unknown.

- Family band size ranged from two to eleven individuals (mean = 6.2 ± 0.21[SE]). Family bands were generally comprised of a single adult male, one to five females (mean = 2.8 ± 0.10), zero to three yearlings (mean = 0.6 ± 0.09) and zero to four foals (mean = 1.5 ± 0.11).
- Bachelor males either occurred alone or in groups of two to eight males (mean = 3.0 ± 0.21).
- Family bands were found to be more stable than bachelor groups and generally consisted of the same members when they were re-encountered. In contrast, bachelor groups generally consisted of different members when re-encountered, although bachelor dyads consisting of two or three members were observed together for several months.
- Within MWR, the formation of zebra herds (multiple bands associating together) was never observed. It is suggested that the benefit of living in herds does not outweigh the costs.

Chapter Three: Stable isotope analysis of the diet of plains zebra

- The average $\delta^{13}C$ values of 34 C_3 browse and 27 C_4 grasses from MWR were determined as -29.11‰ ± 1.26(SD) and -12.86‰ ± 0.85. These distinct values corresponded to the reported range of -22 and -35‰ for C_3 browse species and -10 and -15‰ for C_4 grass species; and acted as the end point values for the stable isotope analysis of plains zebra faeces.
- Plains zebra are predominantly grazers, as their diet consists almost entirely of C4 grasses (84.0 - 100.0%).
- Plains zebra occasionally browse to sustain protein levels, especially when the quality and abundance of grasses becomes limited. A significant variation in the proportion of browse (trees, shrubs and forbs) consumed was observed. During the late wet season plains zebra consumed 1.5% ± 1.59 browse compared to 7.2% ± 3.35 during the early dry season and 10.2% ± 4.39 during the late dry season.
- Despite extensive C3 browse availability, plains zebra demonstrate only moderate dietary plasticity to their reliance on C4 grasses at MWR. Careful management of

grassland habitat and habitat heterogeneity are essential for the persistence of plains zebra, especially during severe seasonal conditions.

Chapter Four: Artificial waterhole dependency of plains zebra

- Plains zebra visited artificial water points (AWPs) during each hourly interval over 24 hours. However, plains zebra utilized artificial waterholes primarily during daylight hours, peaking at 09:00, 13:00 and 14:00.
- Artificial waterholes were utilized more in the dry season, especially the late dry season, compared to the wet season.
- During the late wet season (when natural surface water was most abundant) plains zebra preferred to utilize AWPs at 14:00. During the early dry season there was an increase in 16:00 visitations and during the late dry season plains zebra visited AWPs more often at 20:00. The early wet season displayed an increase in visitations at 09:00.
- 82 interactions were observed around AWPs between plains zebra and 12 other species, in addition to other bands of plains zebra. Bushbuck (*Tragelaphus scriptus*), kudu (*Tragelaphus strepsiceros*), lion (*Panthera leo*), nyala (*Tragelaphus angasii*) and sable (*Hippotragus niger*) did not interact with plains zebra even though they were in close proximity. Buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), elephant (*Loxodonta africana*), waterbuck (*Kobus ellipsiprymnus*), warthog (*Phacochoerus africanus*), yellow baboon (*Papio cynocephalus*) and other plains zebra all initiated behaviour toward plains zebra; whereas plains zebra only initiated behaviour towards warthog, waterbuck, yellow baboon and other plains zebra.
- The total interaction rate between plains zebra and other species was influenced by a change in seasons; as well as the group mass of the interacting species. However, the total interaction rate between plains zebra and other species was not influenced by the mass of individuals of the other species, the group size of the other species, the group size of plains zebra or the band composition of the plains zebra.
- Bachelor groups interacted more frequently with other species at AWPs than did family groups.

Chapter Five: Time budgets and social interactions of plains zebra

- A total of 4048 plains zebra minutes (total band observation minutes X the number of focal animals in each session) were collected.
- Family bands allocated the majority of their daylight time budget to feeding behaviour (41.8% ± 2.36(SE)), followed by resting (18.5% ± 2.21), locomotion (10.9% ± 1.05), vigilance (7.5% ± 0.92), maintenance (2.7% ± 0.92) and social behaviour (1.4% ± 0.33). The remaining 17.3% ± 1.90 was not considered for analysis because animals moved out of sight or were influenced by human presence.
- Vigilance behaviour occupied the largest proportion of bachelor band daylight time budgets (27.0% ± 2.72), followed by locomotion (21.0% ± 2.05), feeding (18.4% ± 2.32), resting (15.4% ± 2.85), maintenance (6.4% ± 1.86) and social behaviour (2.4% ± 0.68). The remaining 9.7% ± 1.74 of bachelor band daylight time budgets was not considered for analysis because animals moved out of sight or were influenced by human presence.
- The feeding behaviour of family bands was most significantly influenced by a change in seasons ($F_{3,144} = 10.27$, $p < 0.001$), with 43.5% ± 15.78 more daylight time allocated to feeding during the early wet season than the early dry season. Feeding was also significantly influenced by the presence of a foal ($F_{1,69} = 11.25$, $p < 0.001$) and age ($F_{2,48} = 6.23$, $p = 0.02$) – but to a weaker extent than a change in seasons. Females with foals spent 20.0% ± 5.58 more daylight time feeding than females without foals. Whereas, foals were observed feeding 17.3% ± 6.74 more than adult zebra. The feeding behaviour of bachelors was not influenced by any of these predictors.
- The resting behaviour of family bands was also significantly influenced by the season ($F_{3,130} = 6.06$, $p < 0.001$); however, unlike feeding the amount of time allocated to resting was significantly lower during the late wet season than during the early dry and late dry season; suggesting that feeding and resting behaviour exhibit compositional trade-offs. On the other hand, the resting behaviour of bachelor bands was not influenced by season, but rather by the body condition of bachelors ($F_{1,64} = 5.28$, $p = 0.03$). The time allocated to resting decreased as the body condition of bachelors improved.
- Vigilance behaviour of family bands was influenced by both the age of zebra ($F_{1,68} = 5.83$, $p = 0.02$) and time of day ($F_{2,142} = 3.21$, $p = 0.04$). Foals spent 8.6% ± 3.50 less time

being vigilant when compared to adult zebra. Furthermore, during 08:00 - 12:00h more time was allocated to vigilance than during 12:01 - 16:00h or 16:00 - 20:00h.

- In comparison to family bands, the vigilance behaviour of bachelors bands was significantly influenced by the time of day ($F_{2,64} = 8.01$, $p < 0.001$); with bachelor bands allocating more time being vigilant during 16:01 - 20:00h than 08:00 - 12:00h or 12:01 - 16:00h. Bachelor bands' vigilance behaviour was also influenced by season ($F_{2,64} = 4.14$, $p = 0.02$); as they spent more time vigilant during the early dry and late dry season, than the early wet season.
- Between individuals, non-agonistic social behaviour and mutual grooming were the most commonly observed social behaviours expressed. Non-agonistic social behaviour occurred at a rate of 6.1 acts/hour for bachelor bands and 2.3 acts/hour (including mutual grooming) for family bands. Whereas agonistic interactions occurred 1.8 times/hour in bachelor bands as compared to 0.5 times/hour in family bands
- Our results suggest that the daylight time budgets of plains zebra were influenced by their environment and energy requirements; and that seasonal variation in time spent feeding may indicate a behavioural change to nocturnal feeding or could reflect a lack of adequate forage availability.

6.3 Critical assessment of research findings

In Chapter One, it was stated that the current study will aim to provide fundamental information on how Majete's reintroduction of 174 plains zebra has performed, provide insights into future reintroduction projects, and enhance our knowledge on how pioneer zebra populations establish themselves. It will also aim to improve our understanding on how zebra are limited by or exploit their resources, which will help managers better understand zebra carrying capacity of MWR. Yet, whether these aims were met need to be critically assessed:

During this study, fundamental information on how Majete's reintroduction has performed was provided. It was established that the reintroduction efforts has resulted in the successful establishment of a population, and that the population reflects the social structure and organization found in established populations. Due to the success of this specific reintroduction project, future zebra reintroductions should follow a similar design and implementation. Suitable habitat and protection from overhunting is also critical for ensuring the success after reintroduction. However, results of this study suggesting that the biased sex ratio and lack of herd formation may be an artefact of the founding population structure (which was more female-baised) in concert with environmental factors. Therefore, decisions on which animals form the founding populations must be balanced between management goals, costs, and priorities, and the intended naturalness of the future population.

This study also improved our understanding of how zebra are limited or exploit their resources. It was determined that zebra in MWR are predominantly grazers, but occasionally browse. The contribution of C3 browse (trees, shrubs and forbs) to the diet of zebra increased as the seasons progressed from wet to dry. Yet, despite extensive C_3 browse availability at MWR, zebra demonstrated only moderate dietary plasticity to their reliance on C_4 grasses. As such, careful management of grassland habitat and habitat heterogeneity are essential for the persistence of zebra, especially during severe seasonal conditions. The study also determined that plains zebra in MWR allocated significantly less time to feeding than zebra elsewhere, especially during the dry season. The results therefore suggest that MWR may not adequately include both summer and winter feeding areas. In order to aid the conservation of zebra in MWR, the expansion of the reserve to include winter feeding habitats may be needed or feeding may need to be supplemented during extremely dry years or after extreme fires to prevent zebra mortalities.

Plains zebra were also found to utilize artificial waterholes primarily during daylight hours, peaking at 09:00, 13:00 and 14:00. The frequency of visitations to artificial waterholes were significantly different by season, with plains zebra sightings at AWPs increased during the dry season, especially the late dry season, compared to the wet season. The results from this study indicate that in order to overcome the shortage of natural surface water during the dry season (since no rainfall occur during this time of the year), the provision of water in the form of AWPs in MWR is crucial to prevent mortalities of zebra and possibly other water-dependent species, especially water-dependent grazers. The increase in zebra sightings at artificial waterholes during the dry season also demonstrates the importance of AWPs toward ensuring the future persistence of plains zebra in arid and semi-arid regions of Africa.

Even though this study has achieved the broad aims, various shortcomings have been recognized. Future research can address these problems indentified, as well as provide a greater in-depth analysis.

6.4 Management recommendations

The incorporation of demographic, dietary and behavioural knowledge into conservation efforts are vital for ensuring the future persistence of wildlife and preventing the destructive effects of habitat fragmentation, resource competition and climate change (Boyd, Scorolli, Nowzari & Bouskila, 2016; King, Asa, Plucháček, Houpt & Ransom, 2016). It can also enable scientists to address both theoretical and applied questions (i.e. how does fertility control or reintroductions affect the welfare of animals?) and assist with determining a species' influence and position in an ecosystem (Buchholz, 2007; King *et al*., 2016; Ransom & Cade, 2009). Therefore, it is important to incorporate the findings of this study into the development and execution of suitable management actions for plains zebra in MWR.

The recent enlistment of plains zebra from Least Concern to Near Threatened on the IUCN Red List enhances the need for a conservation and management plan for plains zebra that will ensure their perseverance not only in MWR, but throughout Africa (King & Moehlman, 2016). To develop suitable management actions, developers and conservationists need to understand the relationship between wildlife behaviour and the environment; as well as human needs. This will allow conservationists to determine if the behaviour repertoires of a species are large enough to cope with changes in its environment or if human intervention is needed (Curio, 1998). Apart from understanding the science of coping, management and conservation agencies also need to understand what motivates people to change their attitude towards conservation. In other words, what returns are expected by the landholders for preserving wildlife? People will only change if they are engaged and empowered (Rubenstein, 2010).

Since plains zebra were extirpated from MWR before the establishment of a public-private partnership (PPP) between African Parks (Pty) Ltd. and the Malawi Department of National Parks and Wildlife (DNPW), a Conservation and Management Plan is needed to ensure their survival. A proposed Conservation and Management Plan for plains zebra in MWR as adapted from the Conservation and Management Strategy for Grevy's zebra (*Equus grevyi*) in Kenya by the Kenya Wildlife Service (2012) is presented in Figure 6.1.

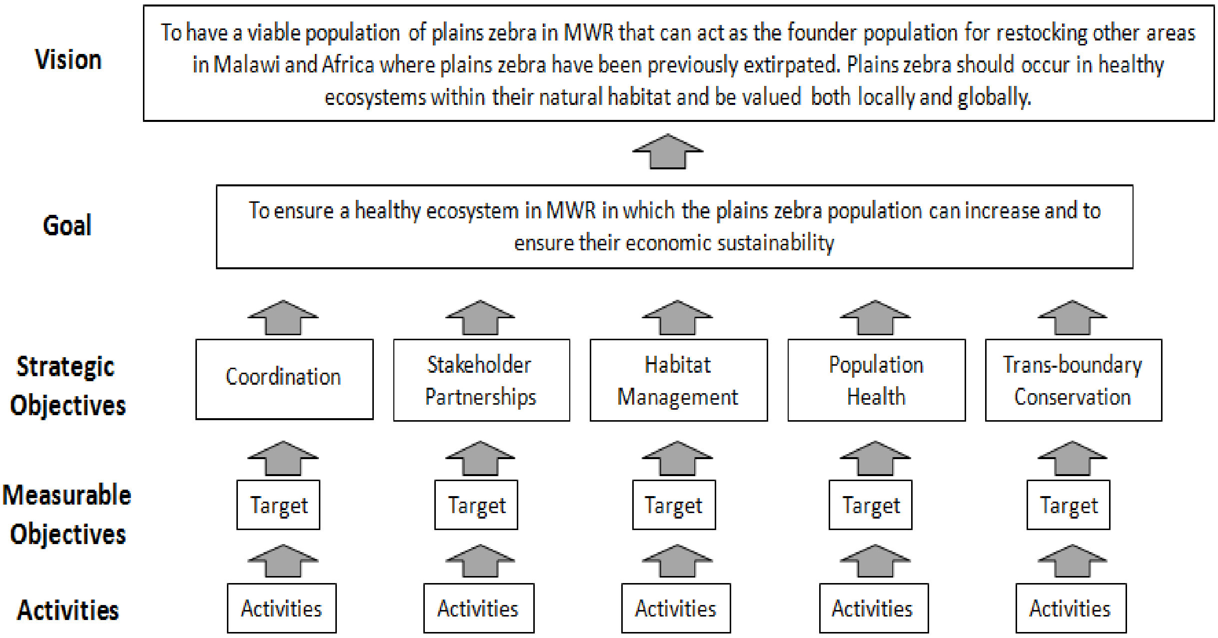

Figure 6.1: Proposed Conservation and Management Plan structure for plains zebra in MWR, Malawi (adapted from Kenya Widlife Service, 2012)

The Conservation and Management Plan needs to strive towards encompassing a realistic vision and goal. Depending on the ultimate objective, plains zebra management can take many forms. The goal of management can either be one or a combination of the following: i) to control populations, ii) to reduce human-wildlife conflict or iii) to maintain populations. However, these aims can be conflicting, and differences in objectives can lead to a variance in management practices (Nuñez, Scorolli, Lagos, Berman & Kane, 2016). Furthermore, for the Conservation and Management Plan as suggested in Figure 6.1 to be successful, its implementation needs to be reviewed annually, and revised if necessary. The Conservation and Management Plan for plains zebra can be adapted for other herbivores, as well as other protected areas. Currently the plan identifies five strategic objectives as suggested by the Kenya Wildlife Service (2012):

1. Coordination of the implementation of conservation and management strategies
2. Enhancement of stakeholder partnerships (including local communities, donors, government agencies and other conservation agencies) in plains zebra conservation
3. Enhancement of plains zebra conservation and habitat management
4. Establish a program for monitoring and managing plains zebra population health
5. Enhancement of trans-boundary plains zebra conservation including translocation and reintroduction projects

In order to assess if specific interventions are required, the Conservation and Management Plan for plains zebra in MWR also requires a better understanding of the reserve's population growth and carrying capacity. However, calculating carrying capacities are challenging as the carrying capacity of an area can fluctuate annually due to a variation over time in the abundance and quality of resources (Ransom *et al*., 2016). Any attempt to model population growth and determine the carrying capacity of MWR's plains zebra should consider the nonlinear density dependence typical of wild equid populations (Gilpen & Ayala, 1973, Ransom *et al.,* 2016). To inform such modelling, however, this population first requires population estimates that are derived from defensible, statistically-based survey techniques. To date, the two aerial surveys conducted have been uncorrected direct counts, which may be informative enough for many management objectives but likely insufficient for accurate projections of growth and carrying capacity. If such metrics are desired by managers, then aerial surveys must employ methods such as mark-resight, simultaneous double-count, line transect surveys, or techniques that combine these methodologies, to address detection bias and estimate the number of zebra that are present but undetected by observers (Williams, Nichols & Conroy, 2002).

Despite the unknown true population size of zebra at MWR, it is clear from the minimum direct aerial counts that the population is growing rapidly. The expected lag in population growth following reintroduction has clearly transitioned to the rapid growth period typical of an equid population that is approaching carrying capacity. Rowan (2000) suggested a carrying capacity of 300 plains zebra for MWR in 2000. This is however an underestimate of the current carrying capacity as the habitat and environmental conditions of MWR has vastly improved since then due to the establishment of a PPP between African Parks (Pty) Ltd. and the DNPW in 2003 which has resulted in improved management, law enforcement and infrastructure, as well as a restored ecosystem (Wienand, 2003). In addition, the proposed threshold of 300 zebra was reached shortly after the 2012 count, with no apparent decrease in population growth at the last count of 571 in 2015. Close observation and management is required at present, such that managers can assess the need to control zebra population numbers with changing resource conditions. Some minimum broad actions are recommended by Hack, East and Rubenstein, (2002) and Stears, Shrader and Castley (2016) that:

1. The demographics and growth of the plains zebra population continues to be monitored.
2. That annual risk assessments be conducted.
3. The genetic diversity of the population be assessed and managed as needed.
4. Economic alternative utilisation strategies are investigated.
5. That the removal of fences or the establishment of corridors between protected areas be investigated to allow for the migration of plains zebra.
6. That a temporal variation in the spatial distribution of AWP's be maintained in order to ensure habitat heterogeneity through a variation in habitat use and movements of animals across the landscape.

A number of management actions may assist to address the potential issues identified by this study. It is important that a combination of these suggestions be practiced in order to successfully manage and conserve plains zebra in MWR. Some management options are as follows:

6.4.1 *Culling*

MWR is a small, fenced reserve with a predator population far below carrying capacity, that tend not to select for zebra (as discussed in Chapter 2; Briers-Louw, 2017). Therefore, management will need to maintain the population as previous studies have indicated that zebra are more limited by top-down than bottom-up processes (Grange, 2006). Both population growth and adult sex ratio (female-biased at 0.8:1.0), indicate a lack of environmental pressures and therefore zebra may need to be removed from MWR if the population continues to increase past the reserves carrying capacity and start to effect other species negatively (for example sable and hartebeest). One option is culling. This is a management practise that aims to control population numbers by killing individual animals indiscriminately or systematically (selecting for a specific sex, age or reproductive state) depending on the goal (Nuñez *et al*., 2016). Transitioning the adult sex ratio at MWR closer to parity could decrease population growth. It should be noted that indiscrimate culling may disproportionately remove bachelor males who form bands of 2-8 individuals at MWR. This would have little or no effect on population growth due to the polygynous mating system and social organization structure presented in Chapter 2. The general stability of family bands and prevalence of affiliative behaviours within them (see Chapter 5) also suggests that culling individuals from bands could have far-reaching adverse social implications. As such, any culling approach for zebra should focus on removal of entire family bands, as is considered for elephants, a species with similar social bonds (Lötter, 2006). This approach would also remove more females than males from the system, thus facilitating a more equitable sex ratio.

Even though culling can prove highly effective in reducing plains zebra numbers, culling tends to be viewed as distasteful by the majority of the public and according to African Parks (Pty) Ltd.'s policies, no culling is allowed in MWR (Forrer, 2016; Nuñez *et al*., 2016). If culling is the only resort available in order to control the spread of disease among plains zebra (for example anthrax) then it would be advised to reconsider it as a management option.

If culling is required, general recommendations are to: 1) determine demographics, distribution and movement patterns of plains zebra; 2) describe the problem; 3) determine a variety of management options; 4) engage stakeholders; 5) implement approved actions; 6) quantify changes in demographics, distribution and movement patterns, as well as success of controlling population numbers; 7) if needed repeat steps one to six; and 8) continue to maintain and control population numbers without culling (Dobbie, Berman & Braysher, 1993).

In addition to these eight steps, it is advised to evaluate population density, environmental conditions, grazing availability and time of year, as well as individual conditions, genetics and behaviour so that animals in a weaker or poorer condition be culled first. This will result in more informed decision making (Nuñez *et al*., 2016).

6.4.2 *Sales: game ranches and game auctions*

In order to control plains zebra population numbers, a number of individual plains zebra can also be cropped and sold annually (Stears *et al*., 2016). If the population biology of MWR's plains zebra population is understood, this can be done in an ecologically sustainable fashion and an income of $300 – $400 can be expected for an individual in good condition (Rowan, 2000; Rubenstein, 2010). As a general guideline, for every fifty plains zebra, three individuals could be cropped annually (Macdonald, 2006; Rubenstein 2010). Thus, for a population of 571 plains zebra, 34 may be cropped in a single year and a gross profit of $10 200 – $13 600 can be made. To date, the selling of plains zebra from other protected areas have not affected wild, plains zebra populations negatively. There is however no way in controlling that the animal will not end up in the hunting industry once sold (Stears e*t al*., 2016). The selling of plains zebra can also be viewed as distasteful by the public.

Recommendations for sales follow the same considerations as outlined for culling. Both actions result in loss of animals from the system and implications for social and population dynamics considerations are the same.

6.4.3 *Contraceptives*

The public unacceptability of culling or selling wild animals that live in protected areas has resulted in the development of wildlife contraceptives (Kirkpatrick & Turner, 1991; Nuñez *et al*., 2016). Specifically, immuno-contraceptives are management tools that cause a temporary infertility in females by either suppressing gonadotropin secretion (GnRH vaccination) or prevent the fertilization of eggs by stimulating the immune system (PZP vaccination) (Dalin, Andresen & Malmgren, 2002; Sacco, 1977). Even though contraceptives are effective at accomplishing infertility in females and have minimal side-effects, they can be costly (Ransom e*t al*., 2014a; Turner, Liu, Flanagan, Byunum & Rutberg, 2002). Re-vaccinations of immuno-contraceptives are also necessary in order to maintain infertility in females and the use of such agents are not always practical (Killian, Thain, Diehl, Rhyan & Miller, 2008). Furthermore, the success of contraceptives resulting in lower population levels can take a substantial amount of time and contraceptives are probably not effective at reducing large, open populations (Conservation Breeding Specialist Group, 2006; Ransom, Powers, Hobbs & Baker, 2014b).

At MWR, any fertility control efforts for zebra should target females. The polygynous mating system indicates that most fertilization is likely from the single band stallion (Chapter 2), with little reproductive contribution from bachelor males. It should be noted, however, that numerous side-effects to female fertility control are possible, including destabilization of bands and changes to social behaviours (Nunez *et al*. 2016). It is unknown how the social organization depicted in Chapter 2 or the behaviour depicted in Chapter 5 would change with the application of fertility control agents to female zebra.

6.4.4 *Translocation and reintroduction*

Translocation and reintroduction is a management practice that involves the movement of animals from high density to low density areas in order to establish or reinforce population size, or to assist with maintaining genetic diversity (Hrabar & Kerley, 2013). Translocation and reintroduction projects should always be planned, put into practice and assessed according to the IUCN/SSC's "Guidelines on Reintroduction and Other Conservation Translocations" (Kaczensky *et al*., 2016). However, these projects can be costly and logistically challenging (IUCN/SSC, 2013).

Within MWR, reintroductions and translocations have proven highly successful in establishing and maintaining a sustainable plains zebra population within the reserve since their extirpation from MWR by 1985 (Patton, 2011). A total of 174 plains zebra were reintroduced into the reserve between 2004 and 2009 from Liwonde National Park, Malawi, and Zambian game ranches (A. Uys & P. Ndadzela, personal communication, February 2, 2017). In 2015, the population was estimated to stand at approximately 571 individuals and in July 2016, 23 plains zebra were translocated from MWR to Liwonde (Appendix 1.2). An additional 27 plains zebra were translocated to Liwonde in July 2017, as well as 25 plains zebra to Nkhotakota Wildlife Reserve, Malawi (African Parks (Pty) Ltd., 2017). The success of MWR's plains zebra reintroduction and translocation project can also be attributed to the fencing of the reserve, improved management, law enforcement and a healthier reserve ecosystem since the involvement of African Parks (Pty) Ltd. (Gyöngyi, 2011; Wienand, 2013). This reiterates the importance of addressing threats prior to reintroduction, as well as having a founder population larger than 100 animals (Kaczensky *et al*., 2016).

Within the immediate future, translocations are a viable option to control and manage MWR's plains zebra population as numerous conservation measures are ongoing within Malawi, including the reintroductions of plains zebra in to protected areas from which the species were extirpated or are occurring at extremely low densities (King & Moehlman, 2016).

Recommendations for translocations follow the same considerations as outlined for culling. Like culling and sales, translocation actions result in loss of animals from the system and implications for social and population dynamics considerations are the same. Translocations for reintroduction, however, have the synergetistic aspect of promoting removal of intact family bands because those are the most desired social groups for establishing a new population.

6.4.5 *Established predator population*

Even though predators are present within MWR, they currently occur at densities far below the suggested carrying capacity made by Briers-Louw (2017). Managers could wait for predator populations to increase or could reintroduce more predators that select specifically for plains zebra (generally lions and hyenas) to control the plains zebra population in a natural and publically acceptable manner (Grange & Duncan, 2006). Predation generally proves to be a successful tool in managing plains zebra population size, as it has been determined that plains zebra are more sensitive to top-down than bottom-up processes (Grange, 2006). However, in MWR lion and hyena populations' select for plains zebra at a frequency of 2.98% and 8.29%, respectively (Briers-Louw, 2017), and contribute to 4.25% of the total biomass consumed by lion and 14.04% of total biomass consumed by hyena (Briers-Louw, 2017). Learned behaviour may strongly influence which species predators feed on (Ransom *et al.*, 2016). In addition, maintaining ecologically sustainable numbers of plains zebra and predators can prove challenging (Rubenstein, 2010). Yet, without an established predator population selecting for plains zebra, human intervention will be never-ending in controlling plains zebra population numbers (Nuñez *et al.*, 2016).

As predators become established, or are reintroduced, the location and use of artificial waterholes (see Chapter 4) may be important toward managing distribution of zebra across MWR in concert with distribution and resource selection of predators. Distribution of both species is critical toward managing population size as predators begin to establish individual home ranges in the reserve and select certain species and/or demographics of their prey. Maintaining artificial waterholes in the areas of the reserve that are high in predator density may promote depredation of zebra when population control is needed. In the short term, it may also be possible to minimize depredation when needed by maintaining artificial waterholes in low predator density areas while closing them in high predator density areas, so long as the open AWPs remain outside of predator home ranges. This will of course alter prey selection, and managers must consider how they may affect other prey species populations.

6.4.6 *Supplemental feeding*

Despite the fact that plains zebra numbers in MWR may soon need to be controlled, plains zebra may possibly require supplemental feeding during particularly poor environmental conditions (for example during extreme droughts). It is clear from our dietary analysis (Chapter 3) that plains zebra in MWR exhibit very little dietary plasticity and can not likely exploit browse in sufficient quantities to overcome extreme poor conditions. Supplemental feeding is a technique that can be used in the management of large herbivores and can assist with re-distributing populations; maintaining high densities of herbivores; enhancing the reproductive performance of species, through enhancing their body condition; or to provide animals with food during critical times to prevent starvation induced mortalities (Kowalczyk *et al*., 2011; Putman & Staines, 2004).

As explained in Chapter Five, plains zebra in MWR have uncharacteristically low feeding rates during the dry season, and it is unknown if that is compensated by nocturnal feeding or possibly as a result of the limited abundance of grasses during this particular season within the reserve. Regardless, supplemental feeding can assist with alleviating the stress associated with limited food availability. However, if not managed correctly, supplemental feeding can result in unnatural population growth (Nuñez *et al*., 2016). If the population needs to be drastically reduced, supplemental feeding would prevent much needed starvation induced mortalities during the dry season. Supplemental feeding can also prove costly, logistically challenging and less favoured by management and conservation agencies (Nuñez *et al*., 2016). Therefore, supplemental feeding must be practised with caution and requires collaboration between management and research (Kowalczyk *et al*., 2011). If supplemental feeding were to be considered at MWR, feed should consist of high quality native C_4 grasses, which zebra are most adapted to exploit.

6.4.7 *Expansion of the reserve*

Plains zebra are predominantly grazers and migrate across seasons to follow the abundance of grasses (Rubenstein, Cao & Chi, 2016; Schoenecker, King, Nordquist, Nandintsetseg & Cao, 2016). Their seasonal movements are therefore influenced by a change in summer and winter habitat diet quality and abundance. However, fencing causes landscape fragmentation and has the potential to alter their migration routes (Ekernas & Berger, 2016; Naidoo *et al*., 2014). Yet, fencing can assist management to effectively reduce human-wildlife conflict (Woodroffe, Hedges & Durant, 2014). Any fenced-off conservation area should be large enough to encompass both winter and summer feeding zones (Penzhorn & Novellie, 1991). As suggested in Chapter Five, MWR might not be large enough to include both these feeding habitats as the feeding rates of plains zebra within the reserve was lower than expected during the dry season. Therefore, the expansion of the reserve to include both summer and winter feeding habitats might alleviate the problem identified in Chapter Five. Bartlam-Brooks, Bonyongo and Harris, (2011) observed that the removal of an estimated 100km fence in 2004 (that was constructed in 1968) allowed plains zebra in northwest Botswana to re-establish their migration route within a four year time frame.

MWR's only possible option for expansion is to include Lengwe National Park (887km^2), since surrounding communities supporting over 140 000 people restricting the expansion of the reserve to other areas. However, Lengwe has a poor infrastructure and experience high levels of poaching due to a lack of law-enforcement and the park's proximity to Mozambique. In addition, Lengwe's vegetation is highly degraded. Local communities would also need to be translocated in order to connect the two protected areas (C. Hay, personal communication, January 31, 2017). These problems would need to be addressed prior to the expansion of MWR and can prove both costly and logistically challenging. Therefore the expansion of MWR to include Lengwe National Park is highly unlikely.

6.4.8 *Habitat heterogeneity: opening and closing of artificial waterholes*

In semi-arid regions, the provision of water in the form of AWPs is frequently used by management and conservation agencies as a management technique (Smit, Grant & Devereux, 2007). AWPs have the potential to increase wildlife densities and can help conserve wildlife in semi-arid and arid ecosystems (Ayeni, 1977; Chamaillé-Jammes, Fritz & Murindagome, 2007; Owen-Smith, 1996, Redfern, Grant, Gaylard & Getz, 2005). However, the provision of surface water can result in vegetation destruction around AWPs, landscape homogenization and an alteration in predator-prey relationships (Cain, Owen-Smith & Macandza, 2011; Chamaillé-Jammes, Charbonnel, Dray, Madzikanda & Fritz, 2016; Sirot, Renaud & Pays, 2016). Therefore, water provision policies should have a defined goal and vision, with a sustainable implementation and action plan (Smit & Grant, 2009).

It has been suggested that in order to maintain habitat diversity and resilience, artificial waterholes should alternate between being open and closed (Smit & Grant, 2009). The opening and closing of waterholes according to Chamaillé-Jammes *et al.* (2016) can be successful if: 1) an adaptive management framework is applied; 2) reliable predictions under different management scenarios on the distribution of herbivores can be made and 3) the surface water provision policy can be adjusted accordingly to a change in environmental pressures and herbivore distribution. Deciding annually which AWPs to open and close can be problematic. Therefore, it is recommended that management efforts should not result in an unnatural situation, but rather mimic natural conditions during the wettest time of the year (Chamaillé-Jammes *et al*., 2007).

Additionally, to decrease the likelihood of animals aggregating around waterholes and causing the destruction of vegetation, many medium-sized waterholes should be used to disperse impacts rather than a few large waterholes that may localize more extensive damage (Ayeni, 1975). The interaction of species at AWPs in MWR did appear to be influenced by season, and zebra specifically were the recipients of displacement behaviours from many species (Chapter 4). Our study did not measure time spent by various species at AWPs or impacts to vegetation. It would be expected that if AWPs were larger in size and fewer in number, any potential negative effects from such interactions on zebra would magnify.

AWPs should be located in lower lying areas, rather than along an altitudinal gradient, to prevent soil erosion and piosphere effects (Owen-Smith, 1996). It is also been proposed that waterholes be spaced at least three times the distance animals will travel on a daily bases to water in order to maintain a mosaic-like landscape with adequate foraging areas available during drought conditions (Smith, Grant & Devereux, 2007). On average, plains zebra travel an estimated 5km to water daily; therefore 15km spacing between AWPs and natural water points is recommended (Owen-Smith, 1996; Smit *et al.*, 2007). If waterholes are managed correctly, herbivore grazing can maintain habitat heterogeneity and decrease the intensity of habitat management (Kampf, 2002). Spatial distribution of AWPs across the reserve should also consider the possible effects on predator resource selection as outlined above.

6.5 Conclusion

From the data presented, it is clear that no single management strategy is best, but that a combination of management techniques will need to be implemented and practised in order to ensure the successful management of plains zebra within MWR, since it is a small fenced reserve with limited predator numbers (Nuñez *et al.*, 2016). To guarantee that the most suitable management strategies are identified, selected and implemented, a Conservation and Management Plan for plains zebra must first be constructed, with a clearly defined vision and goal – that is realistically achievable (Kenya Wildlife Service, 2012). However, limited tools are available for managers to control and conserve plains zebra populations, especially when policies and public opinions are restricting (Nuñez *et al*., 2016). Every important decision made should involve all the necessary stakeholders and the costs and benefits of each option should be weighed along with its efficacy and feasibility (Kenya Wildlife Services, 2012; Nuñez *et al*., 2016).

The information gained from this study has enhanced our current understanding of the ecology of plains zebra and is crucial for advancing the conservation of plains zebra, but conservation is not achieved by information alone (Ekernas & Berger, 2016). Therefore, the information gained from this study should be encompassed into conservation efforts for it to be of significant value.

Challenges regarding the conservation of wild plains zebra will persist. Further scientific research will be needed to ensure the long-term sustainability of plains zebra.

Conservationists will also need to identify new, creative solutions that will address the problems identified, since access to water and forage is once again identified as a key issue regarding the conservation of plains zebra (Ekernas & Berger, 2016). Nevertheless, the successful reintroduction and establishment of plains zebra in MWR provides hope for the conservation of plains zebra across Africa, as well as other wild equids.

6.6 References

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Appendices

Appendix 1.1

Table A.1 Details of Majete Wildlife Reserves'wildlife reintroductions between 2003 and 2016, along with the aerial survey estimates of 2015.

Species	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**Total**	**Aerial count (2015)**
Black Rhino	2				6									1	**9**	**16**
Buffalo	120	100				86									**306**	**1319**
Eland		20				32	25								**77**	**320**
Elephant				70		64	83								**217**	**389**
Hartebeest		4		10		15	30								**59**	**80**
Impala	216					210		311						400	**1137**	**2000**
Leopard									2	4					**6**	**-**
Lion										3					**3**	**-**
Nyala	6	15				38									**59**	**300**
Sable	100					153		99							**352**	**1337**
Warthog	60					98									**158**	**1500**
Waterbuck	98					198		106							**402**	**1782**
Zebra		37	50	9		38	40								**174**	**571**

Appendix 1.2

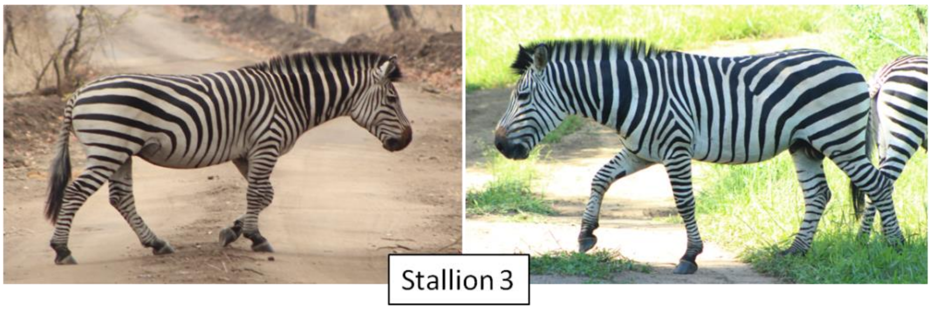
Due to an excess of herbivores within Majete Wildlife Reserve (MWR), animals were translocated from MWR to Liwonde National Park and Nkhotakota Wildlife Reserve in June and July 2016, as well as June and July 2017. Both Liwonde National Park and Nkhotakota Wildlife Reserve are under African Parks (Pty) Ltd.'s management since 2015 and animals were translocated to these protected areas to assist with restoring wildlife to these reserves.

Table A.2 Details of wildlife translocations from Majete Wildlife Reserve to Liwonde National Park and Nkhotakota Wildlife Reserve, Malawi, between 2016 and 2017.

	Liwonde National Park		Nkhotakota Wildlife Reserve		Private Game Ranches / Other	
Species	**2016**	**2017**	**2016**	**2017**	**2017**	**Total**
Eland	25	23		25	19	**92**
Elephant				154		**154**
Hartebeest		7				**7**
Impala					50	**50**
Kudu			99		11	**110**
Sable		19	200			**219**
Warthog					16	**16**
Waterbuck			202	101	10	**313**
Zebra	23	27		25	12	**87**

Appendix 2

An example of a well-known zebra family band in Majete Wildlife Reserve's zebra database. Each family band stallion was given a unique code and the same code acted as the family name for the rest of the band members. Foals were named after their mothers. Each individual member of the family band was sexed and aged and both the left and right side stripe patterns were used to identify individuals.



Stallion 3

Stallion 3 - Mare 1

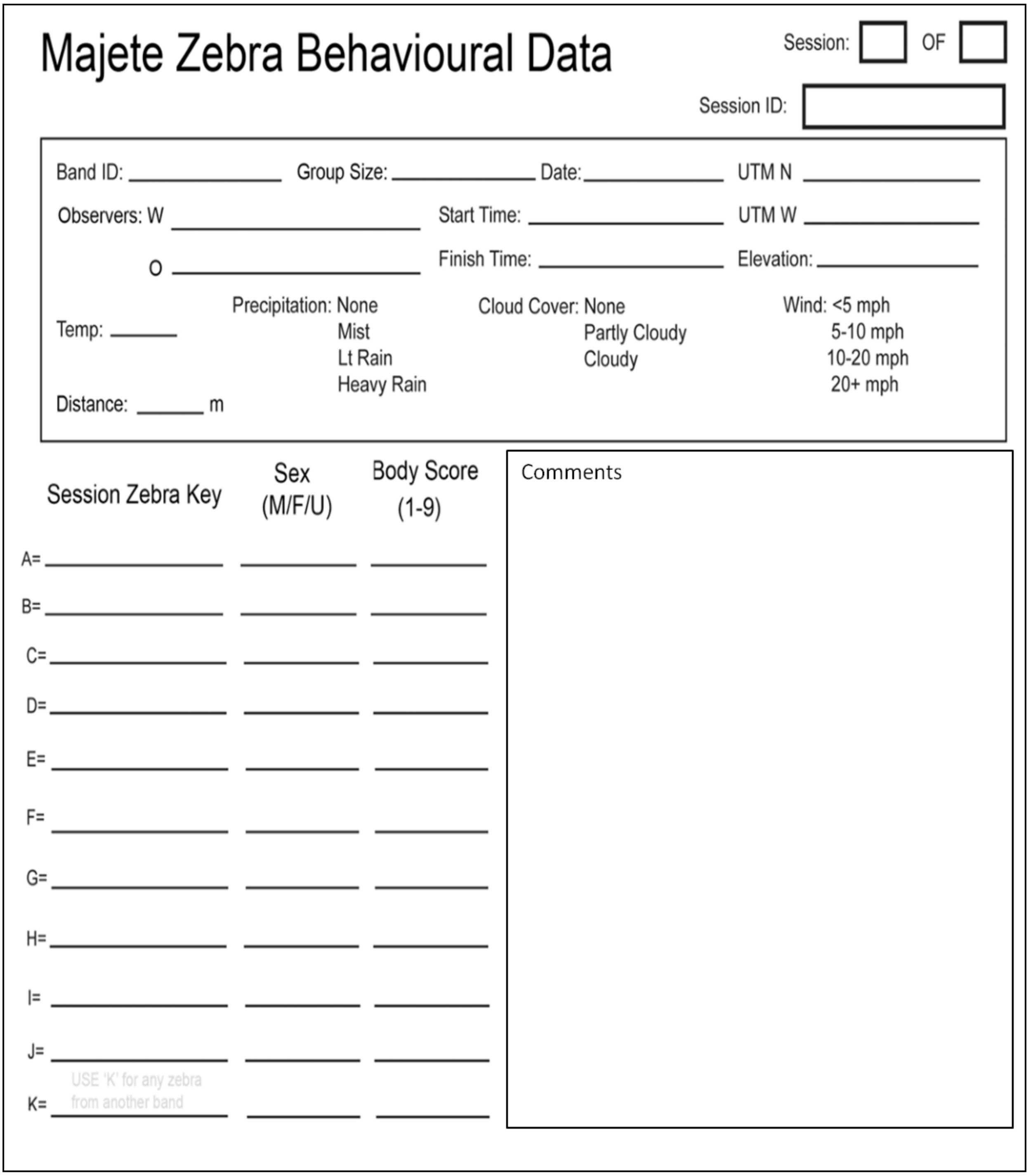
Stallion 3 - Mare 1 – Foal 1

Stallion 3 - Mare 2

Stallion 3 - Mare 2 – Foal 1

Appendix 3

An example of a blank datasheet used to collect time budget and social behaviour of zebra at Majete Wildlife Reserve. The first page of the datasheet was completed before a video recording of the session commenced. Pages two and three were only completed after the video session was terminated and was completed by watching and analysing the video recording of the specific session.



Majete Zebra Behavioural Data

Session: ☐ OF ☐

Session ID: ☐

Band ID: ____________ Group Size: ____________ Date: ____________ UTM N ____________

Observers: W ____________ Start Time: ____________ UTM W ____________

O ____________ Finish Time: ____________ Elevation: ____________

Temp: ______

Precipitation: None
Mist
Lt Rain
Heavy Rain

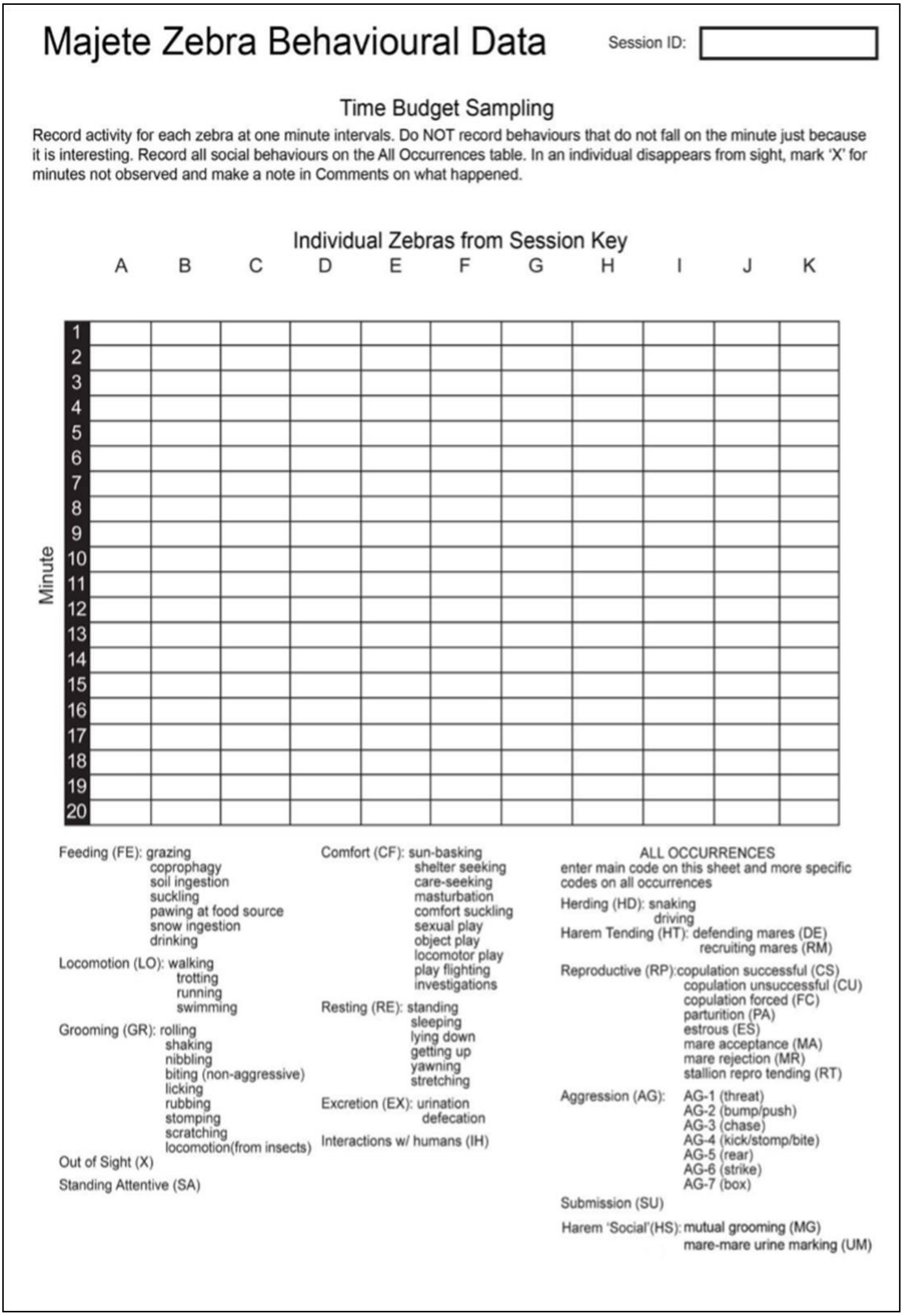
Cloud Cover: None
Partly Cloudy
Cloudy

Wind: <5 mph
5-10 mph
10-20 mph
20+ mph

Distance: ______ m

Session Zebra Key	Sex (M/F/U)	Body Score (1-9)
A=		
B=		
C=		
D=		
E=		
F=		
G=		
H=		
I=		
J=		
K= USE 'K' for any zebra from another band		

Comments



Majete Zebra Behavioural Data

Session ID: ☐

Time Budget Sampling

Record activity for each zebra at one minute intervals. Do NOT record behaviours that do not fall on the minute just because it is interesting. Record all social behaviours on the All Occurrences table. In an individual disappears from sight, mark 'X' for minutes not observed and make a note in Comments on what happened.

Individual Zebras from Session Key

Minute	A	B	C	D	E	F	G	H	I	J	K
1											
2											
3											
4											
5											
6											
7											
8											
9											
10											
11											
12											
13											
14											
15											
16											
17											
18											
19											
20											

Feeding (FE): grazing
coprophagy
soil ingestion
suckling
pawing at food source
snow ingestion
drinking

Locomotion (LO): walking
trotting
running
swimming

Grooming (GR): rolling
shaking
nibbling
biting (non-aggressive)
licking
rubbing
stomping
scratching
locomotion(from insects)

Out of Sight (X)

Standing Attentive (SA)

Comfort (CF): sun-basking
shelter seeking
care-seeking
masturbation
comfort suckling
sexual play
object play
locomotor play
play flighting
investigations

Resting (RE): standing
sleeping
lying down
getting up
yawning
stretching

Excretion (EX): urination
defecation

Interactions w/ humans (IH)

ALL OCCURRENCES

enter main code on this sheet and more specific codes on all occurrences

Herding (HD): snaking
driving

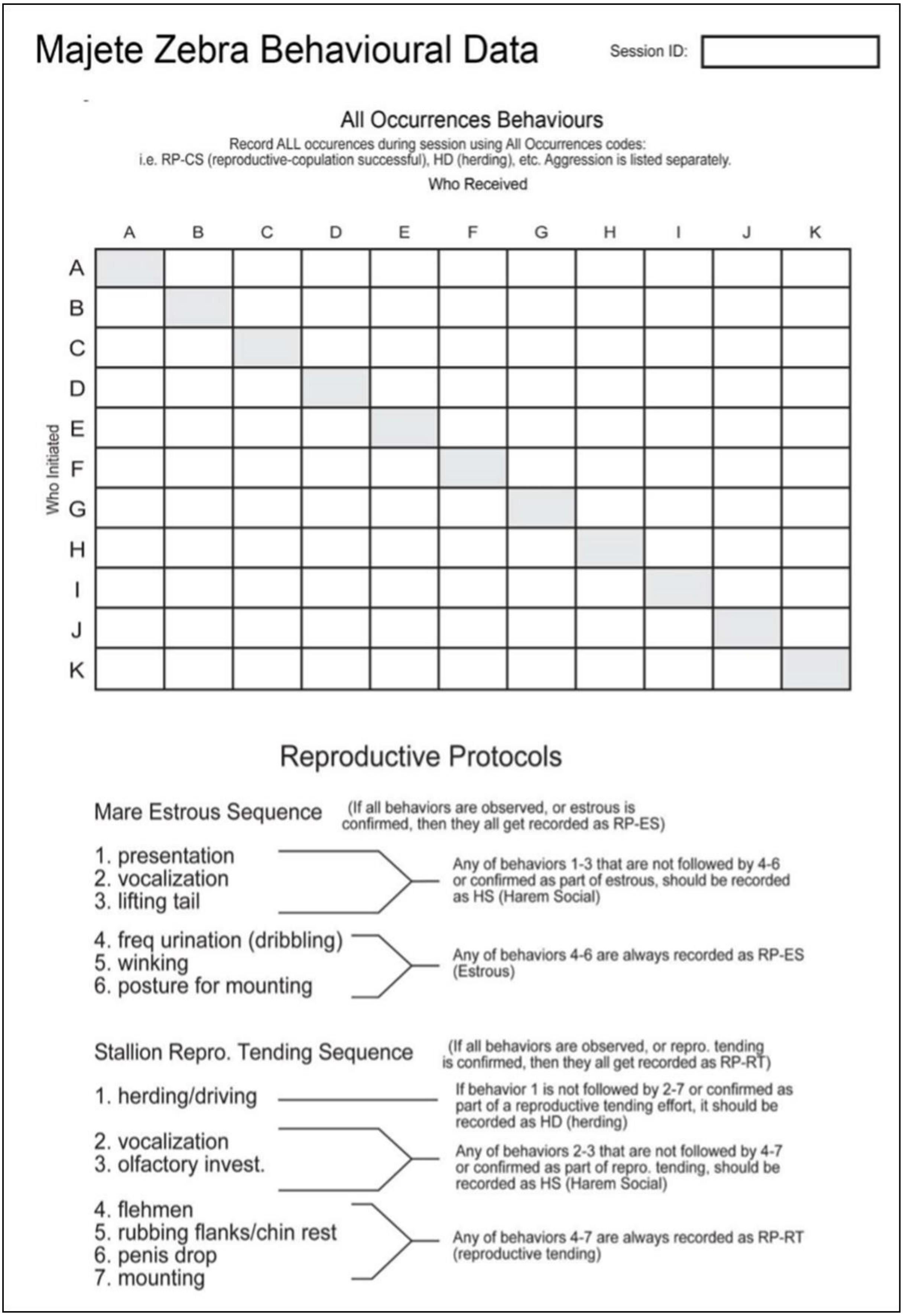
Harem Tending (HT): defending mares (DE)
recruiting mares (RM)

Reproductive (RP):copulation successful (CS)
copulation unsuccessful (CU)
copulation forced (FC)
parturition (PA)
estrous (ES)
mare acceptance (MA)
mare rejection (MR)
stallion repro tending (RT)

Aggression (AG): AG-1 (threat)
AG-2 (bump/push)
AG-3 (chase)
AG-4 (kick/stomp/bite)
AG-5 (rear)
AG-6 (strike)
AG-7 (box)

Submission (SU)

Harem 'Social'(HS): mutual grooming (MG)
mare-mare urine marking (UM)



Majete Zebra Behavioural Data

Session ID: ☐

All Occurrences Behaviours

Record ALL occurences during session using All Occurrences codes:
i.e. RP-CS (reproductive-copulation successful), HD (herding), etc. Aggression is listed separately.

Who Received

Who Initiated

	A	B	C	D	E	F	G	H	I	J	K
A	▨										
B		▨									
C			▨								
D				▨							
E					▨						
F						▨					
G							▨				
H								▨			
I									▨		
J										▨	
K											▨

Reproductive Protocols

Mare Estrous Sequence

(If all behaviors are observed, or estrous is confirmed, then they all get recorded as RP-ES)

1. presentation
2. vocalization
3. lifting tail

Any of behaviors 1-3 that are not followed by 4-6 or confirmed as part of estrous, should be recorded as HS (Harem Social)

4. freq urination (dribbling)
5. winking
6. posture for mounting

Any of behaviors 4-6 are always recorded as RP-ES (Estrous)

Stallion Repro. Tending Sequence

(If all behaviors are observed, or repro. tending is confirmed, then they all get recorded as RP-RT)

1. herding/driving

If behavior 1 is not followed by 2-7 or confirmed as part of a reproductive tending effort, it should be recorded as HD (herding)

2. vocalization
3. olfactory invest.

Any of behaviors 2-3 that are not followed by 4-7 or confirmed as part of repro. tending, should be recorded as HS (Harem Social)

4. flehmen
5. rubbing flanks/chin rest
6. penis drop
7. mounting

Any of behaviors 4-7 are always recorded as RP-RT (reproductive tending)