

**Establishing genetic and environmental
parameters for ostrich
(*Struthio camelus domesticus*)
growth and slaughter characteristics**

by

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DECLARATION

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

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ABSTRACT

The ostrich industry is a predominantly quantitative industry; focused mainly on the production of large numbers of slaughter birds for maximum meat and leather yield. Competing in the international market in the current economic environment necessitates a more qualitative approach. Productivity and product quality are aspects that need to be improved in order to stay competitive and economically viable. Genetic parameters for ostrich slaughter traits are lacking, however, and breeding programs are yet to be developed. Data on quantitative and qualitative production and slaughter traits from a commercial ostrich breeding flock was consequently analysed to establish the relative importance of genetic and non-genetic influences on these traits. Genetic and environmental (co)variances as well as estimates of heritability, genetic and phenotypic correlations were estimated for and among the various traits using standard software for multi-trait genetic analyses.

Substantial variation, high and favourable genetic correlations as well as moderate to high heritability estimates were found among, and for distinguished body weight traits of growing ostriches. Heritability estimates of 0.14, 0.22, 0.33, 0.43 and 0.43 for 1-month, 4-month, 7-month, 10-month and 13-month-old ostrich weights were estimated in a five-trait animal model analysis.

All carcass component weight traits, with the exception of the weight of the liver, showed significant genetic variation. No significant maternal permanent environmental variance was evident for these traits. Heritability estimates ranged from 0.21 (for subcutaneous fat weight) to 0.45 (for neck weight) in multi-trait analyses. The only potentially unfavourable correlation was a high genetic correlation between live weight and subcutaneous fat weight, as fat is considered as a waste product in the present system. The heritability estimates for individual muscle weights ranged from 0.14 to 0.43, while the genetic correlation between these weights and pre-slaughter live weight were all positive, ranging from 0.59 to 0.82.

When meat quality traits were analysed it was evident that lightness (L^*) and ultimate pH (pH_u) showed significant genetic variation, with heritability estimates of 0.37 and 0.42, respectively. L^* and pH_u were negatively correlated (-0.65 ± 0.19). Since pH is an indicator of various meat quality parameters, it could be considered as an appropriate selection criterion for enhanced meat quality.

With the exception of skin grading and crown length, all quantitative and qualitative skin traits showed significant genetic variation. Nodule traits were accordingly moderate to highly heritable. A negative, but favourable, correlation between weight and hair follicle score was ascertained, as hair follicles is a defect that should be selected against.

This study demonstrated that sufficient genetic variation exists for most slaughter traits to allow sustained genetic progress for these traits, should it be desired as part of the overall selection objective. Combining some of the current economically important slaughter traits in a provisional selection index, it was clear that

weight and crust skin size contributed most to monetary gain (approximately 54 and 38%, respectively). It was also demonstrated with this simple index that monetary gains in slaughter bird production should be easy to achieve at all levels of production performance and data recording.

OPSOMMING

Die volstruisbedryf is hoofsaaklik 'n kwantitatiewe bedryf wat meerendeels fokus op die produksie van groot getalle slagvolstruise vir die produksie van vleis en leer. Siende dat die bedryf hoofsaaklik op uitvoere fokus, word aanvaar dat 'n verandering in strategie na 'n meer kwalitatiewe benadering nodig is, in ag geneem die huidige ekonomiese situasie en marktoestande. Produktiwiteit sowel as produkgehalte moet in ag geneem word vir die bedryf om lewensvatbaar te bly. Daar is egter 'n gebrek aan genetiese parameters vir volstruisslageienskappe, terwyl doeltreffende teeltstelsels nog ontwikkel moet word. Data van kwantitatiewe en kwalitatiewe produksie- en slageienskappe is gevolglik van 'n kommersiële volstruis teeltkudde verkry en ontleed om die relatiewe belang van genetiese en nie-genetiese effekte op die eienskappe te kwantifiseer. Genetiese- en omgewings (ko)variensies, asook beramings van oorerflikheid sowel as genetiese en fenotipiese korrelasies, is vervolgens vir en tussen die onderskeie eienskappe beraam deur van standaard sagteware vir veelvuldige-eienskap genetiese ontledings gebruik te maak.

Aansienlike variasie, hoë en meestal gunstige korrelasies, sowel as matige tot hoë oorerflikhede, is tussen en vir die onderskeie ligaamsgewigte van groeiende volstruise gevind. Oorerflikheidsberamings van 0.14, 0.22, 0.33, 0.43 en 0.43 is vir 1-maand, 4-maande, 7-maande, 10-maande en 13-maande-oue volstruise in 'n vyf-eienskap dieremodel ontleding gekry.

Alle karkaskomponentgewigte, met die uitsondering van die gewig van die lewer, het betekenisvolle genetiese variasie getoon. Oorerflikheidsberamings het tussen 0.21 (vir onderhuidse vetgewig) en 0.45 (vir nekgewig) gevarieer in veelvuldige-eienskapontledings. Die enigste moontlike ongunstige korrelasie was tussen liggaamsgewig en onderhuidse vetgewig, siende dat vet as 'n afvalproduk gereken word in die huidige stelsel. Die oorerflikhede van die gewigte van individuele spiere het van 0.14 tot 0.43 gevarieer, terwyl die genetiese korrelasies tussen hierdie gewigte en voorslaggewig deurgaans positief was, met waardes wat van 0.59 tot 0.82 gewissel het.

Tydens die ontleding van vleisgehalte eienskappe was dit duidelik dat ligtheid (L^*) en uiteindelijke pH (pH_u) genetiese variasie getoon het, met oorerflikheidsberamings van onderskeidelik 0.37 en 0.42. L^* en pH_u was negatief gekorreleerd op die genetiese vlak (-0.65 ± 0.19). Aangesien pH 'n aanduiding is van verskeie vleisgehalteparameters, kan dit moontlik as 'n indirekte seleksie-kriterium vir verbeterde vleisgehalte gesien word.

Alle kwantitatiewe en kwalitatiewe veleienskappe het genetiese variasie getoon, met die uitsondering van velgradering en kroonlengte. Knoppie-eienskappe van die veerfollikels op die vel was ooreenstemmend matig tot hoog oorerflik. 'n Negatiewe, maar gunstige, genetiese korrelasie is tussen liggaamsgewig en haarfollikelpunt beraam, siende dat haarfollikels 'n defek is waarteen daar geselekteer moet word.

Hierdie studie dui op voldoende genetiese variasie vir die meeste slageienskappe om voldoende genetiese vordering te verseker indien dit verlang sou word. Sommige van hierdie eienskappe wat tans van ekonomiese belang is, is vervolgens in 'n voorlopige seleksie-indeks gekombineer. Dit was duidelik dat liggaamsgewig en velgrootte die meeste tot monetêre vordering bygedra het (onderskeidelik ongeveer 54 en 38%). Dit is vervolgens aangetoon dat monetêre vordering maklik haalbaar behoort te wees op alle vlakke van produksieprestasie en data-aantekening.

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RESEARCH OUTPUTS STEMMING FROM THE STUDY

Peer-reviewed publications that appeared in journals and conference proceedings:

- Meyer, A., Cloete, S.W.P., Van Wyk, J.B. & Van Schalkwyk, S.J., 2004. Is genetic selection for skin nodule traits of ostriches feasible? *South African Journal of Animal Science* 34, 29-31.
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Congress contributions:

- Meyer, A., Cloete, S.W.P., Van Wyk, J.B. & Van Schalkwyk, S.J., 2004. Is genetic selection for skin nodule traits of ostriches feasible? *Book of Abstracts of the 2nd Joint Congress of the Grassland Society of Southern Africa and the South African Society of Animal Science*, Goudini, p. 59.
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CHAPTER 1

General introduction

Ostriches were domesticated around 1863 (Smit, 1964), mainly as a result of the usage of ostrich feathers in women's fashions (Osterhoff, 1979). The South African ostrich industry is built mainly around the South African 'Black' ostrich (*Struthio camelus domesticus*) - a synthetic breed that was bred from various crosses between the North African ostrich (*S. c. camelus*) and the southern African ostrich (*S. c. australis*) for the production of good quality feathers. Other strains of ostriches that are now also used, to a lesser degree, for commercial ostrich production are Zimbabwean Blue ostriches (*S. c. australis*), found naturally in Zimbabwe, the Kalahari, Namibia and northern South Africa), and Kenyan Red ostriches (*S. c. massaicus*), found naturally in Kenya and Tanzania.

After the collapse of the feather industry in 1881 and again in 1914 (Van Zyl, 1996), a resurgence of interest in ostriches during the 1960's subsequently saw extensive ostrich farming being transformed into an intensive industry (Van Zyl, 2001). Around 1975 the emphasis shifted away from feathers towards the production of leather (Van Zyl, 1996). By the late 1980's the more intensive ostrich industry was well established and based on the production of leather, meat and feathers (Van Zyl, 2001), which are still today the main products obtained from ostriches. The industry is now by large a slaughter industry, with the production of slaughter birds being the main purpose of most ostrich farming enterprises.

The industry is largely export-driven with approximately 90% of ostrich meat and 70% of ostrich leather being exported (Anon., 2012). In South Africa approximately 240 000 ostriches are slaughtered annually, with South Africa holding more than 70% of the global market share (Anon., 2012). This is highly dependent on disease status however, with numbers dwindling when ostriches are culled due to avian influenza outbreaks such as the 2011 outbreak which saw more than 50 000 birds being culled.

Research efforts have focused on the high value products according to market trends over the years, focusing on ostrich feather quality during the feather boom early in the 20th century and moving toward leather and meat research at the end of the twentieth century as these products gained commercial value. These research findings have been reviewed on a regular basis (Sales & Oliver-Jones, 1996; Sales & Horbanczuk, 1998; Cooper, 2001; Sales, 2002; Hoffman, 2005; Engelbrecht *et al.*, 2009; Polawska *et al.*, 2011; Cloete *et al.*, 2012) and interested readers are referred to these literature sources for more detailed information.

After the collapse of the feather market, which previously encouraged structured breeding for feather quality, the ostrich industry has become a predominantly quantitative industry, focusing on the production of high

volumes instead of product quality. Since competing in the luxury international market after the deregulation of the South African industry in 1995, the need for a more qualitative approach has once again become important, however. Improvement of productivity and product quality are aspects that necessitate attention and can benefit the industry markedly.

Product quality is largely determined at farm level where the birds are being raised. Angel (1996) argued that modifying on-farm management could improve product quality and productivity. However, limited improvement is possible with nutrition and other management practices (Meyer, 2003). Genetic selection may provide the industry with more scope for progress, since many traits are thought to be under genetic control, which would make additive progress possible. The success of genetic improvement as a tool for improved productivity has been well illustrated in other livestock species.

At this stage, the industry is characterised by large variation pertaining to growth and production. This can be related to the short domestication history of the ostrich and a lack of selection due to the flock breeding practice that are commonly employed in the industry. More than 90% of breeding ostriches are kept in large breeding flocks, with no traceability system between chicks and parents, making performance recording and genetic selection impossible. Little is consequently known about the genetic basis of the observed variation in production traits.

Genetic parameters for most ostrich production traits are very scarce, which make selection for favourable traits exceedingly difficult. This is especially true for ostrich slaughter traits. Moreover, defined breeding objectives and industry breeding structures are absent (Cloete *et al.*, 2008) and effective breeding programs are yet to be developed.

Knowledge of genetic parameters for economically important traits is a prerequisite for the formation of effective genetic improvement programs and accurate parameter estimates are needed so as to ensure that the highest possible genetic gains are obtained (Mukherjee & Frairs, 1970). There is consequently an urgent need to determine accurate genetic parameters for slaughter traits to establish selection objectives for the industry.

Preliminary results indicate that progress is feasible in a range of ostrich production traits, and that selection is a viable option (Cloete *et al.*, 2008). Many leather traits are reportedly related to production traits, which will make selection for leather traits based on a phenotypic production trait possible. Cloete *et al.* (1998) reported a high between-animal correlation between live weight and certain skin traits, for instance. Selection based on live weight can therefore possibly benefit certain desirable leather traits as correlated responses.

Although direct selection is more effective than indirect selection in most cases, indirect selection can lead to faster genetic progress when the trait representing the indirect selection criterion has a higher heritability, is highly correlated to the trait to be improved and has a wide range of expression (McGuirk & Atkins, 1980).

Indirect selection is particularly important for traits that are difficult to measure accurately, costly to measure or not expressed in all environments (McGuirk & Atkins, 1980). Leather and meat traits would fall into these categories because it can only be measured after slaughter, therefore it could potentially benefit from an indirect selection strategy.

The primary focus of the ostrich industry today is the commercial production of ostriches for their products – meat, leather and feathers. The meat and skin of the ostrich is responsible for approximately 90% of the income from an ostrich slaughtered for the export market, each contributing between 30 and 60% to the income, depending on market conditions and product quality. The quality of skins, in particular, has a mentionable impact on the price of the commodity. The ideal would therefore be to breed ostriches for combinations of these product traits. It is notable that, whereas the genetics of ostrich leather traits based on preliminary analyses did form part of the review on ostrich leather by Engelbrecht *et al.* (2009), no review paper involving the genetics of ostrich meat traits is available. This can be attributed to a lack of suitable data and research pertaining to this topic.

There is also a general lack of information on the relationships between growth and slaughter traits. This study consequently aims to estimate variance components for growth, meat and skin traits for ostriches for use in a preliminary selection index to potentially improve the quality of slaughter birds.

The information needed to construct a selection index include phenotypic standard deviations for each trait, the phenotypic and genetic correlation between each pair of traits, the heritability of each trait, and the relative economic value for each trait (Hazel, 1943). Heritability estimates can also help in making decisions regarding the type of mating system that will maximize the rate of improvement realized by selection, while genetic correlations between traits give an indication of the extent to which two traits are controlled by the same genes, permitting one to predict the correlated response of one trait to selection for a different trait (Kinney, 1969). Genetic parameters (including heritability estimates and genetic correlations), as well as environmental parameters, will consequently be estimated for growth and slaughter traits to investigate the possibility of genetic improvement for slaughter production.

The heritability of feather weights of mature ostriches has already been estimated (Brand & Cloete, 2009). In contrast to the high value of feathers harvested from mature ostriches, the feathers of slaughter ostriches are of little value. Price determination is done according to a complicated grading system whereby feathers from slaughter birds are often regarded as worthless, depending on their stage of development as well as overall quality. Feathers will therefore not be included in this study of slaughter traits.

The South African ostrich industry has access to sufficient genetic resources in terms of pedigreed flocks for an investigation of this nature. The Oudtshoorn Research Farm is one of the only institutions with a breeding structure and recording system that can generate data suitable for genetic evaluation and research. It is thus important to use this resource to maintain and extend a competitive edge, and to take the lead in genetic improvement for the ostrich industry.

Data on quantitative (yield) and qualitative production traits are recorded routinely for the commercial ostrich breeding flock maintained at the Oudtshoorn Research Farm. Records for these birds were supplemented with additional slaughter and skin data and linked to the available pedigree information. The data were edited and manipulated prior to statistical analysis to establish the relative importance of genetic and non-genetic influences on a range of production and slaughter traits recorded or generated from the data. Genetic and environmental (co)variances as well as estimates of heritability, genetic and phenotypic correlations were estimated for and among the various traits. The results of this study will contribute towards a selection strategy for the ostrich industry.

This thesis consists of a number of manuscripts. These manuscripts address the following issues in separate chapters:

- Genetic and environmental factors that affect live weight at different ages in a pair-bred ostrich flock, using a five-trait animal model,
- Genetic and environmental factors affecting quantitative ostrich meat traits,
- Genetic and environmental factors affecting qualitative ostrich meat traits,
- Genetic and environmental factors affecting qualitative and quantitative ostrich skin traits,
- Genetic and environmental factors affecting qualitative ostrich skin traits assessed by subjective scoring,
- The combination of slaughter traits in a preliminary selection index for slaughter bird production,
- And, finally, conclusions and recommendations pertaining to future research.

As can be seen on page IX the study already yielded some publications. Some of the publications had inconclusive outcomes, such as where nodule size was assessed objectively (Meyer *et al.*, 2004; Cloete *et al.*, 2006). This line of research was thus not pursued further. In other cases, preliminary results on growth and leather traits were reported from smaller databases or data with a less than optimal structure in terms of age distribution and representation of animals in contemporary groups (Engelbrecht *et al.*, 2005; 2007; 2009; 2011). In this report care was taken to use larger databases or data with a better structure to optimally represent the resource population. It is therefore difficult to relate previous publications to specific chapters, but earlier work is cited where relevant.

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CHAPTER 2

Estimation of genetic parameters for ostrich weight traits using a multi-trait model

2.1 Introduction

Livestock producers aim to improve profitability through increased efficiency. While Van Zyl (2001) showed that an increase in slaughter income is one of the most important factors impacting on profitability in the ostrich industry, growth and feed efficiency also need to be considered pertaining to efficient production and profitability, seeing as profit is a function of both outputs and inputs (Yüksel, 1979; Petite & Davis, 1999; Cloete *et al.*, 2008).

Furthermore, although until rather recently leather contributed the major share of the slaughter income of ostrich producers (Meyer *et al.*, 2002), ostrich meat has since increased in popularity (Hoffman, 2008). Towards the end of the previous decade meat has been just as important as a source of income (Cloete *et al.*, 2008). Ostrich growth rate is therefore an important trait, since it influences age at slaughter and slaughter income through its association with body weight, muscle development and degree of maturity.

Generally, a heavier weight at slaughter would translate into improved financial gains since the unit price for ostrich meat increases as total carcass weight increases in the South African market. Slaughter weight is also positively correlated with other economically important slaughter traits, such as skin size and nodule size (Engelbrecht *et al.*, 2007; 2009). However, feed efficiency decreases substantially with age, with ostriches becoming relatively inefficient after about 11 months of age (Aganga *et al.*, 2003). Feed costs are known to be the single largest cost factor in most livestock production systems, and in the ostrich industry it can be as much as 70 to 80% of production costs (Brand *et al.*, 2000). In theory, by increasing growth rate, one can reduce the rearing time for achieving a desired bodyweight, and improve the efficiency of production through reduced maintenance costs.

While ostriches were traditionally regarded as ready for slaughter within 12 to 14 months of hatching (Cooper, 2000), optimal slaughter weight for meat production is now achievable from eight months of age. Ostriches are generally deemed fast-growing birds (Smith *et al.*, 1995). Unfortunately, large variation in growth rate is common among ostriches (Deeming *et al.*, 1993; Mushi *et al.*, 1998), with birds in the same contemporary groups often not ready for slaughter at the same time. Because most ostrich producers rely

on body weight alone as a criterion for slaughtering (Jarvis, 1998), ostriches are being slaughtered at a wide range of ages, often long after feed efficiency has declined, thus hampering profitability.

In other livestock species growth is known to be under genetic control (Sainz & Cabbage, 1997), with growth traits being moderate to highly heritable (Sainz, 1991). Heritability estimates for body weight in the domestic fowl range from 0.25 – 0.65 (Kinney, 1969; Crawford, 1990) and substantial genetic progress in growth has consequently been made with poultry (Emmerson, 1997), enabling more efficient production and improved profitability.

In the ostrich industry little has been achieved as far as genetic progress is concerned (Petitte & Davis, 1999; Cloete *et al.*, 2004), partly due to a lack of genetic evaluation of performance. Bunter *et al.* (1999) and Bunter & Cloete (2004) were the first researchers to estimate genetic parameters for ostrich weight traits; showing that a genetic basis for ostrich growth existed. However, the latter authors pointed out that the available ostrich data were characterised by random effects that were confounded, thus complicating accurate modelling for estimation of heritabilities and correlations. It was recommended that ostrich breeders should improve their data structures by mixing animals across breeding pairs and increasing the turnover of breeding stock, to improve future parameter estimates.

Continued improvement of data structures (Cloete *et al.*, 2008) and accumulation of data have since made further investigation into genetic parameters for ostrich growth traits possible. Against this background, genetic and environmental (co)variance components and ratios were estimated for and among various ostrich bodyweight traits, making use of more recent data.

2.2 Materials and methods

2.2.1 Data description

Data from South African Black (SAB) ostriches (*Struthio camelus domesticus*) were obtained from the pair-bred ostrich flock maintained at the Oudtshoorn Research Farm near Oudtshoorn, South Africa. This flock had been consistently recorded for pedigree and performance data since 1990 and is the same resource population that was used to obtain most genetic parameter estimates for ostriches to date (Cloete *et al.*, 2008).

The flock was originally developed as a research resource from a donation of 76 commercial SAB breeder birds made by 61 local producers in 1964. The flock have been enlarged and developed over the years, and currently consists of 188 breeding pairs that are maintained and replaced at a rate of approximately 15% per year (Engelbrecht *et al.*, 2008).

Individual breeding pairs are kept in small breeding paddocks of approximately 0.25 hectare. Birds, eggs and chicks are individually identified to enable accurate performance and pedigree recording. Eggs are collected daily and artificially incubated in weekly batches.

Progeny from the flock are reared in similarly aged groups of up to 100 in size and then either slaughtered for research purposes or used for the replacement of breeding birds. Due to facility constraints on the premises, excess day-old chicks are sold to local producers and their data are consequently not available post hatch. Chicks hatched early in the breeding season are mostly retained for growing out in preference to chicks hatched later in the season.

The ostriches are reared in feedlot conditions for most of their life, with ostrich diets and fresh water provided *ad libitum*. Certain batches of chicks have additional access to lucerne pastures up to three months of age.

Five different diets were fed from hatch to slaughter, as suggested by Cilliers (1995), based on the weight of the ostriches. Pre-starter (1-10 kg), starter (10-40 kg), grower (40-60 kg), finisher (60-90 kg) and maintenance (90+ kg) diets, with 12.5, 11.5, 10.5, 9.2 and 7.5 MJ/ME and 23, 19, 15.5, 14 and 12% protein were used until 1998. The specifications for these diets were then changed to contain approximately 14.5, 13.5, 10.5, 9.5 and 7 MJ/ME and 19, 17, 15, 12 and 10% protein, in accordance with the guidelines for the composition of ostrich feeds (Department of Agriculture, 2001). Small adjustments in the rations were made over the years. These changes were unfortunately not documented consistently.

Groups of ostriches were routinely weighed at approximately monthly intervals from day-old onwards. However, farm operations and other constraints (shortage of manpower, weather conditions, time constraints etc.) prevented weighing of all progeny at exact intervals. The exact age at weighing was therefore recorded throughout. All weights within a range of 30 days around the average monthly age were categorised together as one weight trait (i.e. 1-month weight or 30-day weight (15-44 days; abbreviated as W1), 2-month or 60-day weight (45-74 days; W2), etc.).

Five weight traits with 3-monthly intervals were chosen for analyses based on the distribution of records. However, day-old weight, which is generally regarded as a maternal trait, was excluded. Animals with weights recorded for the following age ranges were retained: 15-44 days (W1), 105-134 days (W4), 195-224 days (W7), 285-314 days (W10) and 375-404 days (W13). These ages also represented the whole range of dietary groups, namely pre-starter (W1), starter (W4), grower (W7), finisher (W10) and maintenance (W13) diets.

Weight data from SAB chicks hatched and reared under similar conditions from 1996 to 2008 were used. Data from other genotypes reared in the same contemporary group were excluded due to limited representation per genotype. Each chick had only one record per categorised weight trait, but not all chicks had weight records in each weight category.

The gender of the ostriches was determined by cloacal examination shortly after hatch (Gandini & Keffen, 1985). Where the gender of the chicks was not determined at hatch, it was done either when the ostriches had developed distinguishing dimorphic adult plumage (for birds kept for breeding purposes), or at slaughter by identification of the internal reproductive organs. Ostriches of unknown gender were removed from the data.

The final dataset analysed consisted of 5 208 ostriches, 49.6% males and 50.4% females, representing progeny of 313 sires and 318 dams, mated to each other in 443 unique combinations. One hundred and fifty nine dams had weight records of their own present in the data. The number of progeny per dam varied from one to 92, with an average of 16.4 progeny per dam.

2.2.2 Statistical analysis

Shapiro-Wilk statistics for weight traits were calculated with GenStat (Payne *et al.*, 2010) to test for normality. The ASReml program (Gilmour *et al.*, 2009) was then used for the estimation of fixed effects, and to derive (co)variance components and genetic parameters for the respective weight traits.

The data for each weight trait were analysed by single-trait procedures to identify the fixed effects and random factors to be included in the final operational model. The first analyses involved fitting all the fixed effects and interactions to determine significant ($P < 0.05$) effects, which were used to develop the operational model used in subsequent analyses.

The fixed effects fitted for all traits included the age (in days) of the ostriches at weighing as a linear covariate and linear and quadratic regressions on the age of the female parent (dam age) as covariates. Dam age ranged from two- to 19-year-old.

The models of analysis also included contemporary group and gender and the interaction between them. The effects of year and rearing group were combined into the single effect of contemporary group because not all traits were represented within each year and rearing group. Contemporary groups were defined as year by season of hatch. Season of hatch was defined as follows: early season – July to September, mid-season – October to December, and late season – January to March. Contemporary groups with fewer than 15 records were excluded from the data. Contemporary group was included to account for environmental effects that may have affected chicks being reared together.

Random terms were then added sequentially to the operational model. Direct additive genetic effects and maternal effects of the hen (including maternal additive genetic and maternal permanent environmental effects) were modelled for each weight trait. Maternal permanent environmental effects were also fitted per dam year because the majority of dams had data of progeny hatched in more than one year recorded.

The full linear mixed model (in matrix notation) fitted was as follows:

$$y = X\beta + Z_1a + Z_2m + Z_3pe + Z_3w + e$$

where y was a vector of observations for the respective weight traits and β , a , m , pe and w were vectors of fixed effects, direct and maternal additive genetic effects, maternal permanent environmental effects and within year permanent environmental effects, respectively. X was an incidence matrix relating records to the fixed effects (β), Z_1 , Z_2 and Z_3 were the corresponding incidence matrices relating the observations to the respective random effects, while e was the vector of residual effects. It was assumed that:

$$\text{Var}(a) = A\sigma_a^2; \text{Var}(m) = A\sigma_m^2; \text{Var}(pe) = I\sigma_{pe}^2; \text{Var}(w) = I\sigma_w^2 \text{ and } \text{Var}(e) = I\sigma_e^2,$$

where A was the numerator relationship matrix between animals, I was an identity matrix and σ_a^2 , σ_m^2 , σ_{pe}^2 , σ_w^2 and σ_e^2 were the additive direct, additive maternal, maternal permanent environmental, within year permanent environmental and residual variances, respectively.

The most suitable random effects model for each trait was determined by sequentially testing the addition of one parameter at a time using likelihood ratio tests. An effect was considered significant when its inclusion in the model caused a significant increase in the log-likelihood (LogL). A chi square distribution for $\alpha = 0.05$ and one degree of freedom was used as the critical test statistic (3.841). When 2 times the difference between log-likelihoods was greater than the critical value, the inclusion of the effect was considered significant.

Relationships between the traits and parameter estimates were obtained from a multiple-trait mixed model analysis that included all five traits in a single analysis. Models used for each trait within the multiple-trait analysis were those developed in single-trait analyses. The estimates of (co)variance components from the single-trait analyses were used as starting values for the multiple-trait run. These analyses allowed the calculation of all relevant correlations among traits, together with their respective standard errors.

Results from the multi-trait models were compared using the restricted maximum likelihood (REML) form of the Akaike's information criterion (AIC), that impose penalties according to the number of parameters to be estimated. The model with the lowest AIC values was regarded as the best model.

All analyses included the full pedigree file, consisting of 6 178 individuals, hatched over seven generations, the progeny of 350 sires and 351 dams, mated to each other in 496 unique combinations. The pedigree was built using all available ancestors.

2.3 Results

2.3.1 Descriptive statistics

After editing, the available data consisted of 46 507 weight records for 5 473 ostriches. Figure 2.1 shows the distribution of the raw weight records plotted against age at weighing.

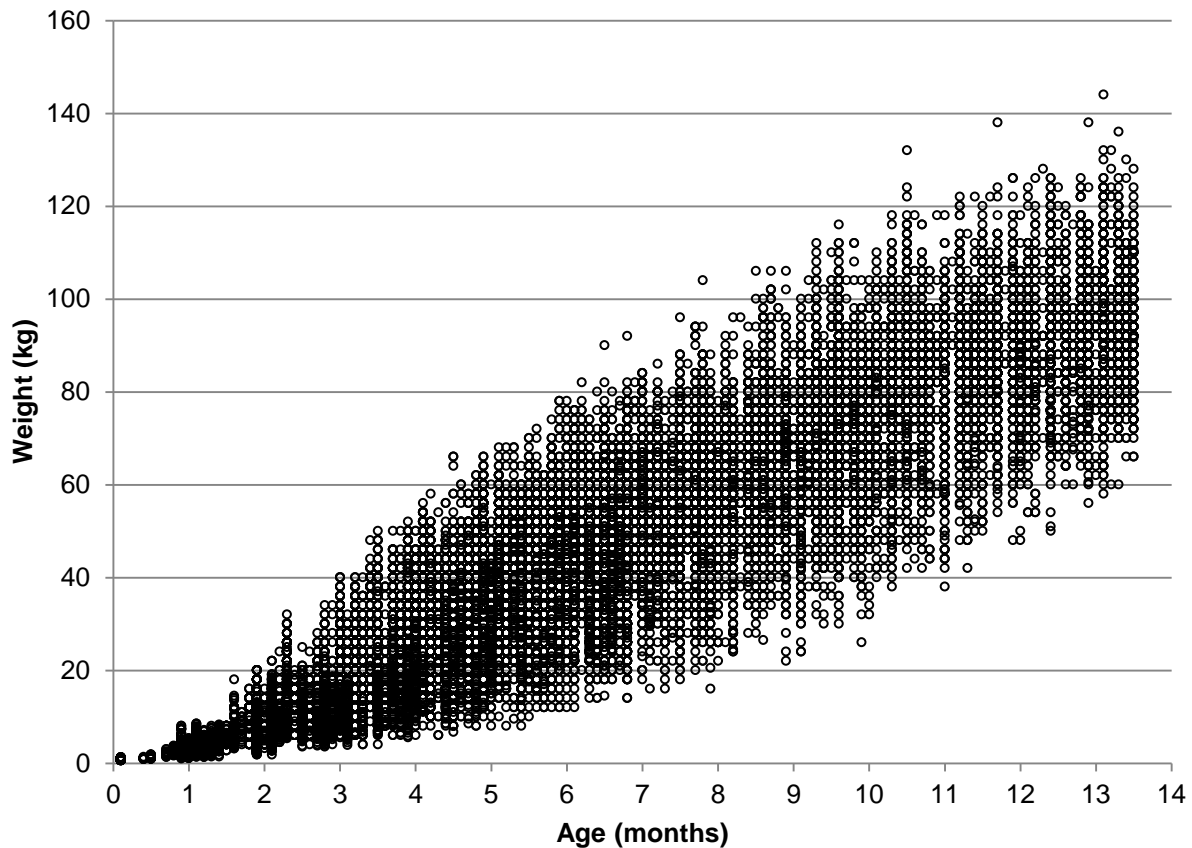


Figure 2.1 A scatter plot depicting the distribution of raw data for ostrich weights as recorded from 1996 to 2008, plotted against age at weighing in days.

Figure 2.2 shows the unadjusted means for ostrich weights by age and the number of records per age category.

The number of records ranged between 1 915 and 4 405 animals for the various traits (Table 2.1). Weight traits were highly variable, with particularly high coefficients of variation for early measurement ages, ranging from 39% for W1 to 41% for W4. Distributions for all weight traits were approximately normal though, with Shapiro-Wilk statistics ranging between 0.93 for W1 and 0.99 for W7, W10 and W13.

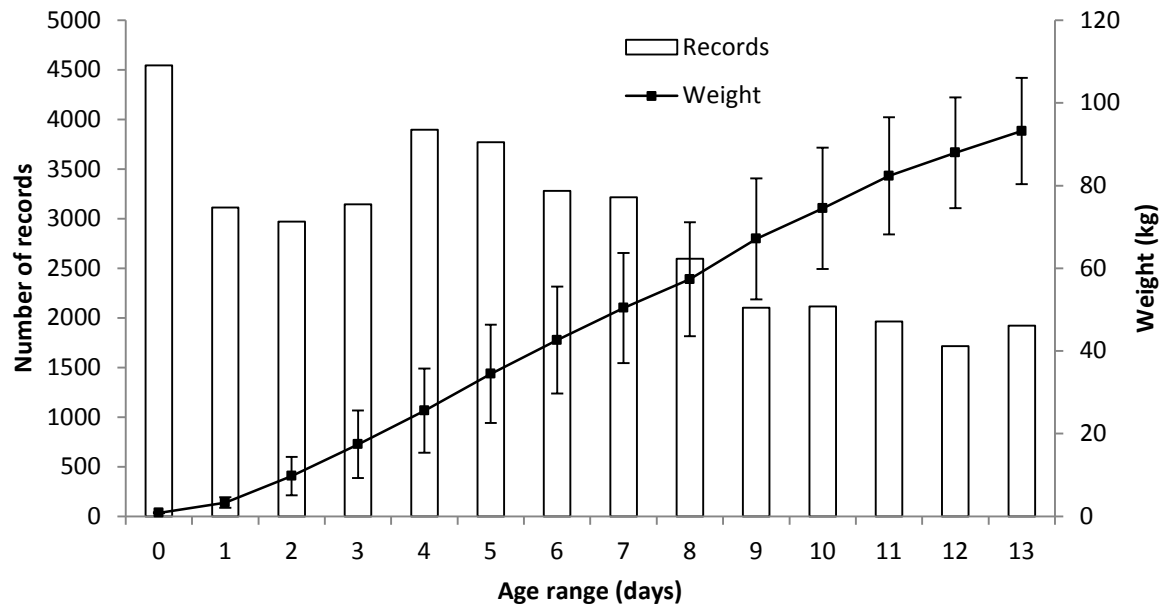


Figure 2.2 Unadjusted mean ostrich weights by age category, also indicating the number of records per category. Vertical lines about the means represent raw data standard deviations.

Table 2.1 Data structure and characteristics for five ostrich weight traits^a

Parameter	W1	W4	W7	W10	W13
Recorded animals (N)	3 408	4 405	3 449	2 409	1 915
Contemporary groups	22	29	28	26	21
No. of sires with progeny recorded	282	311	305	282	279
No. of sires with own record	110	120	89	63	49
No. of progeny/sire	12.1	14.2	11.3	8.5	6.9
No. of dams with progeny recorded	283	314	308	276	272
No. of dams with own record	109	118	111	63	52
No. of progeny/dam	12.0	14.0	11.2	8.7	7.0
No. of maternal grandsires with own record	25	27	20	9	4
No. of maternal granddams with own record	30	29	26	8	6
Mean \pm s.d. (kg)	3.4 \pm 1.3	25 \pm 10	51 \pm 13	75 \pm 14	94 \pm 13
Coefficient of variation (%)	39	41	27	19	14
Range (kg)	1.0 - 9.1	6 - 66	18 - 96	40 - 122	64 - 144
Mean age at weighing (days)	32	120	207	299	391

^a W1: 1-month weight; W4: 4-month weight; W7: 7-month weight; W10: 10-month weight; W13: 13-month weight

Between 1 153 and 3 067 birds had records in other weight classes (Table 2.2). The number of dams with progeny in other weight classes ranged from 25 to 94.

Only 802 ostriches had all five bodyweights recorded; 1 062 had four bodyweights recorded, 1 270 had three weights recorded, 1 444 had two weights recorded and 630 ostriches had only one of the weight traits recorded.

Table 2.2 Distribution of ostrich weight records across five weight traits. Figures on the off-diagonals represent the number of common birds with records. The number of hens with own records is indicated in brackets

Trait ^a	W1	W4	W7	W10	W13
W1	3 408 (109)	3 067 (94)	2 242 (79)	1 536 (42)	1 153 (25)
W2		4 405 (118)	2 854 (83)	2 018 (48)	1 567 (36)
W3			3 449 (111)	2 007 (42)	1 623 (41)
W4				2 409 (63)	1 579 (37)
W5					1 915 (52)

^a W1: 1-month weight; W4: 4-month weight; W7: 7-month weight; W10: 10-month weight; W13: 13-month weight

2.3.2 Fixed effects

Significant fixed effects ($P < 0.05$) for each trait are presented in Table 2.3. The age at weighing was significant for all weight traits. Regressions (\pm s.e.) of weight on age at weighing were 121 ± 5 g/day for W1, 333 ± 15 g/day for W4, 290 ± 23 g/day for W7, 306 ± 28 g/day for W10 and 155 ± 33 g/day for W13.

Table 2.3 Significant fixed effects influencing ostrich live weights, with the coefficient of determination (R^2) indicating the proportion of variation explained by these effects

Trait ^a	Age at weighing	Hen age (L) [#]	Hen age (Q) [#]	Contemporary group (CG)	Gender	CG x gender	R^2
W1	***	n.s.	n.s.	***	n.s.	n.s.	0.42
W4	***	n.s.	n.s.	***	n.s.	n.s.	0.51
W7	***	*	n.s.	***	n.s.	n.s.	0.28
W10	***	n.s.	n.s.	***	n.s.	n.s.	0.19
W13	***	n.s.	n.s.	***	n.s.	n.s.	0.24

Significance levels: * $P < 0.05$ ** $P < 0.01$; *** $P < 0.001$; n.s.: not significant, $P > 0.10$

[#] Depict the linear (L) and quadratic (Q) effects of hen age

^a W1: 1-month weight; W4: 4-month weight; W7: 7-month weight; W10: 10-month weight; W13: 13-month weight

The linear regression of weight on hen age was only significant at W7 ($P = 0.014$), with weight decreasing with -0.17 ± 0.07 kg for an increase of one year in hen age. The quadratic regression of weight on hen age was not significant for any of the traits.

Contemporary group (year by hatch season) affected all weight traits ($P < 0.001$). These often reflect short-term changes in climate and/or management, however, and since such changes are neither predictable nor repeatable, solutions for contemporary group are not reported.

Neither gender nor the interaction of gender with contemporary group was significant for any of the traits and this term was subsequently excluded from the analysis.

2.3.3 (Co)variance components, ratios and correlations

The inclusion of the direct genetic component as a random effect in the operational model resulted in an improved log-likelihood for all traits (Table 2.4). The addition of the maternal permanent environmental effect (pe^2) was also significant ($P < 0.05$) for W1, W4, W7 and W13, with slightly better log-likelihood values compared to the models where the maternal genetic component (m^2) was added instead. The within year effect ($pe^2.yr$) resulted in an improved log-likelihood for W1 when added to a model already including pe^2 , while the inclusion of $pe^2.yr$ as a single random effect additional to h^2 produced the best fit for W4 and W7.

Table 2.4 Log-likelihood values of different models for ostrich growth traits. The best model is shown in bold

Trait ^a	FE	h^2	$h^2 + pe^2$	$h^2 + m^2$	$h^2 + pe^2.yr$	$h^2 + pe^2 + pe^2.yr$	$h^2 + m^2 + pe^2$
W1	-1703.56	-1667.09	-1661.10	-1661.37	-1661.09	-1658.58	-1660.04
W4	-10776.5	-10694.6	-10690.5	-10693.7	-10681.1	-10679.3	-10690.5
W7	-9995.84	-9870.38	-9867.13	-9867.21	-9864.80	-9863.27	-9866.73
W10	-7293.77	-7177.27	-7176.74	-7176.10	-7176.17	-7175.87	-7176.10
W13	-5595.50	-5525.35	-5521.95	-5523.93	-5523.39	-5520.98	-5521.95

FE = fixed effects only; h^2 = FE + animal effect (A); $h^2 + pe^2$ = FE + A + permanent environment of hen (Hen_1); $h^2 + m^2$ = FE + A + additive maternal genetic effect (Hen_A); $h^2 + pe^2.yr$ = FE + A + permanent environment of hen per hen year ($Hen_1.yr$); $h^2 + pe^2 + pe^2.yr$ = FE + A + Hen_1 + $Hen_1.yr$; $h^2 + m^2 + pe^2$ = FE + A + Hen_A + Hen_1

^a W1: 1-month weight; W4: 4-month weight; W7: 7-month weight; W10: 10-month weight; W13: 13-month weight

The random effect of animal was consequently retained for all traits in the multi-trait model, while the maternal permanent environmental effect was retained for W1 and W13, and $pe^2.yr$ were used in the case of W1, W4 and W7, as described above. Heritability (h^2) was estimated at between 0.06 (W1) and 0.45 (W10) for the respective weight traits in single-trait analyses (Table 2.5).

Table 2.5 Variance components and ratios (\pm s.e.) for ostrich growth traits^a as estimated in single-trait analyses

Variance components and ratios	W1	W4	W7	W10	W13
<u>Components:</u>					
Direct additive (σ_a^2)	0.061	6.89	35.3	77.0	32.3
Permanent environment (σ_{pe}^2)	0.033				9.25
Permanent environment per year ($\sigma_{pe.yr}^2$)	0.025	2.70	5.86		
Residual (σ_e^2)	0.861	40.0	84.3	92.9	90.9
Phenotypic (σ_p^2)	0.979	49.6	125.5	169.9	132.5
<u>Ratios:</u>					
Direct additive (h^2)	0.06 \pm 0.03	0.14 \pm 0.03	0.28 \pm 0.05	0.45 \pm 0.06	0.24 \pm 0.08
Dam permanent environment (pe^2)	0.03 \pm 0.02	n.a.	n.a.	n.a.	0.07 \pm 0.03
pe^2 per hen year ($pe^2.yr$)	0.03 \pm 0.01	0.05 \pm 0.01	0.05 \pm 0.02	n.a.	n.a.

^a W1: 1-month weight; W4: 4-month weight; W7: 7-month weight; W10: 10-month weight; W13: 13-month weight

n.a.: not applicable

Maternal permanent environmental variance ratios accounted for between 3% (W1 and W4) and 7% (W13) of the phenotypic variation for the respective ostrich weight traits, while $pe^2.yr$ amounted to 3% (W1) to 5% (W4 and W7) for early weight traits.

Results from a multi-trait model fitting pe^2 for W1 and W13, following the results from the single-trait analysis, indicated that pe^2 became insignificant (0.00 ± 0.01) for W13. The effect of $pe^2.yr$ for W1 and W7 also became insignificant.

A model fitting pe^2 for W1 only and $pe^2.yr$ for W4 only was subsequently fitted. Although the first-mentioned model (based on the parameters included in single-trait analyses) had the highest log-likelihood, the Akaike's information criterion value indicated that the latter model was indeed the best model. The maternal permanent environmental effect for W1 amounted to 0.02 ± 0.01 with this model, while the maternal permanent environmental effect by year was 0.01 ± 0.01 for W4. These effects were consequently also left out for the final analysis. Final results from the multi-trait analyses are reported in Table 2.6.

Table 2.6 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations for ostrich growth traits as estimated in multi-trait analyses

Trait ^a	W1	W4	W7	W10	W13
<i>Additive genetic correlations (h^2 in bold on diagonal)</i>					
W1	0.14 ± 0.03	0.67 ± 0.09	0.40 ± 0.11	0.41 ± 0.11	0.44 ± 0.11
W4		0.22 ± 0.03	0.88 ± 0.03	0.87 ± 0.04	0.87 ± 0.04
W7			0.33 ± 0.04	0.97 ± 0.01	0.88 ± 0.03
W10				0.43 ± 0.05	0.96 ± 0.02
W13					0.43 ± 0.05
<i>Residual correlations (σ_e^2 in bold on diagonal)</i>					
W1	0.858	0.35 ± 0.02	0.30 ± 0.03	0.21 ± 0.03	0.24 ± 0.04
W4		40.3	0.68 ± 0.01	0.51 ± 0.02	0.36 ± 0.03
W7			91.1	0.75 ± 0.01	0.56 ± 0.03
W10				98.1	0.70 ± 0.02
W13					80.7
<i>Phenotypic correlations (σ_p^2 in bold on diagonal)</i>					
W1	0.997	0.41 ± 0.02	0.31 ± 0.02	0.25 ± 0.02	0.28 ± 0.03
W4		51.7	0.73 ± 0.01	0.61 ± 0.01	0.51 ± 0.02
W7			135.1	0.83 ± 0.01	0.68 ± 0.01
W10				171.3	0.81 ± 0.01
W13					141.6

^a W1: 1-month weight; W4: 4-month weight; W7: 7-month weight; W10: 10-month weight; W13: 13-month weight

The heritability estimates obtained from the multi-trait analysis were generally higher than the estimates obtained from the single-trait analysis, increasing until 10 months of age.

Genetic correlations between the weight traits were all positive and significant. Genetic correlations among weights at later ages were all close to unity, with all genetic correlations not involving W1 being 0.87 or greater.

Environmental correlations among weights were somewhat lower at 0.21–0.75, but still highly significant and favourable. Environmental and phenotypic correlations decreased somewhat in magnitude as the time intervals between recordings increased.

2.4 Discussion

2.4.1 Descriptive statistics and fixed effects

The most recorded trait was W4, while the least recorded trait was W13, not surprisingly, as a substantial number of ostriches were slaughtered before they reached 13-months of age. Budgetary and facility constraints, as well as the need for experiments resulted in ostriches being slaughtered at different ages over years. While all the ostriches within a contemporary group that were destined for slaughter were usually slaughtered together, ostriches that were kept for replacement purposes would have more weight records recorded after their contemporaries were slaughtered.

Early weights were highly variable, significantly more so than is common for weights in other farmed livestock species. Marginally lower coefficients of variation were found earlier by Bunter *et al.* (1999) and Bunter & Cloete (2004) for smaller data sets consisting of comparable ostrich weight traits. The larger CV here could be attributed to the availability of more data across years, combined with the presence of a highly significant contemporary group effect (Table 2.3). The contemporary groups consisted of various hatch batches that were pooled, which could have been a source of variation that could not be accounted for. The present analysis also used data from before and after the dietary specifications were revised in 1999, while the previous studies by Bunter *et al.* (1999) and Bunter & Cloete (2004) only used hatch groups grown out with diets formulated according to the initial specifications.

Age at weighing and contemporary group (year and hatching season) explained up to 51% of the variation in weight at younger ages, lending support to Angel's (1996) contention that the growth rate of ostriches was influenced by environmental factors such as temperature. Reduced immunocompetence for ostrich offspring which hatched later in the season was also reported previously (Bonato *et al.*, 1999), which would presumably result in slower growth of these chicks, therefore also indicating a seasonal effect. Gender, on the other hand, was not significant for any of the growth traits, supporting the conclusion of Cloete *et al.* (2002; 2008) that ostriches are not sexually dimorphic for growth and live weight to slaughter.

2.4.2 (Co)variance components, ratios and correlations

The direct additive variance ratio estimates were higher in the multi-trait analysis compared to the single-trait analyses for those traits including pe^2 and/or $pe^2.yr$ as random effects. The repartitioning of variance from pe^2 to h^2 resulted in pe^2 and $pe^2.yr$ becoming very low for W1 and W2 respectively, and negligible for the other weight traits. Bunter & Cloete (2004) accordingly reported that a substantial amount of variation was repartitioned from pe^2 to h^2 in their multi-trait analysis, when compared to the corresponding single-trait analyses. However, the pe^2 estimates remained sizable at between 0.08 for slaughter weight at 14 months and 0.11 for W10 in their study. The h^2 estimates derived in the present study increased with an increase in animal age up to 10 months of age. In contrast, pe^2 was reduced from low to negligible levels with an increase in age. This is not totally unexpected, as it is known that maternal effects decrease in importance as animals age (Nobre *et al.*, 2003). The maternal effect on chick weight is mostly via egg weight in poultry. Zoccarato *et al.* (2004) found that this effect of egg weight on ostrich chick weight decreased as the chick grew, and was no longer significant at an age of 56 days.

The h^2 estimates were higher and had smaller standard errors than the previous estimates obtained from a five-trait analysis for comparable weight traits (Bunter & Cloete, 2004). This increase in parameter accuracy is not unexpected when it is considered that the latter study had much fewer record numbers. Heritability estimates for W10 and W13 were quite similar to the original estimates by Bunter *et al.* (1999) for weight at 10 months (0.42) of age and at slaughter age of approximately 14 months (0.45). However, it needs to be stressed that the latter analysis was based on only between 687 and 843 records for the respective traits, and utilising a model not incorporating pe^2 . When the variance ratio for pe^2 is added to that of h^2 for W10 in the Bunter & Cloete (2004) study the resultant estimate of 0.38 is in fair agreement with the multi-trait estimate of 0.43 in the present study. This repartitioning of variances could therefore have contributed to the slightly improved parameter estimates obtained during this analysis when compared with earlier analyses by Bunter (2002) and Bunter & Cloete (2004). The h^2 for W13 estimated during this study was also in accordance with the h^2 of 0.46 for slaughter weight previously reported by Engelbrecht *et al.* (2005) in a study of slaughter traits. The only other genetic parameters reported for ostrich weight traits were slightly lower, with heritability estimates at 0.12 and 0.33 for weight at 6 months and 12 months of age, respectively (Rosa *et al.*, 2011).

Based on recommendations by Bunter & Cloete (2004), an effort was undertaken in recent years to switch breeder females between males and paddocks. The latter authors reported on the progeny of 191 sires and 195 dams that were paired off in 242 unique combinations. At respectively 313 sires and 318 dams, the number parents contributing to the present study was about 60% larger than those used by Bunter and Cloete (2004), while the number of unique pairs (443) were about 80% more. Although this level of recombination is still not adequate, it could be argued that this would assist in more accurate partitioning of the estimated random effects.

The similarity of log-likelihood values for models including either pe^2 , m^2 , or both, indicated that these effects mostly described the same variation. It was not possible to effectively separate maternal genetic from maternal permanent environmental effects due to an inadequate number of dams and grand dams with weight records themselves. The high correlation between direct and maternal effects in a predominantly full sib design furthermore complicates the separation of variances.

Both Maniatis & Pollott (2003) and Heydarpour *et al.* (2008) argued that complete datasets, with sufficient links between dam performance records and offspring records, as well as sufficient progeny per dam, are required for reliable estimates of maternal genetic parameters in multi-trait situations. With the average generation interval in the research flock approaching eight years (Fair *et al.*, 2012), it is clear that substantial numbers of grand dams with their own records are extremely unlikely. Only 50% of the hens with progeny had weight records of their own (159 out of 318).

Overall, maternal effects did not seem to be very important for ostrich weight traits. The study confirmed moderate to high heritability estimates for weight traits in ostriches, however, indicating that genetic variation is present and that it could be exploited in a well-structured breeding program. Genetic improvement of growth rate via quantitative genetic approaches has been achieved in commercial poultry, resulting in marked reductions in slaughter age (Emmerson, 1997). Body weight heritability estimates for ostriches appear to be similar in magnitude to that of chickens (Koerhuis & Thompson, 1997).

Considering the large magnitude of genetic correlations between weights at different ages, selection for an increase in bodyweight at any particular age (with the possible exception of 1 month of age) is likely to result in an increase in bodyweight at all ages. Genetic correlations between weights recorded from four months onwards were high throughout, in some cases not different from unity, indicating that selection from four months of age onwards will lead to substantive correlated responses in weights at later ages. It would therefore be possible to increase live weight at slaughter age through indirect genetic selection based on earlier weights as indicator traits.

The results are largely consistent with previous studies which also concluded that genetic progress can be made in ostrich live weight when selection is based on weights that can be recorded before slaughter (Bunter & Cloete, 2004; Cloete *et al.*, 2008), but provides more accurate estimates for the use in a selection index.

However, even though genetic selection for improved slaughter weight is feasible, it is important to also consider other economically important slaughter traits, such as skin quality, that may not benefit from an improved slaughter weight or from slaughtering at an earlier age. Both leather and feather income are quality dependant and could influence overall profitability despite of the potentially improved meat income and lower feed costs that would be possible through selection for improved slaughter weight.

2.5 Conclusions

Results from the study suggest that the regime of monthly weighing could be replaced by a more structured approach, such as weighing all ostriches at specific physiological stages, i.e. at approximately 3-months, 5-months, 7-months and 10-months of age. This would result in less recording events, but more consistent recording of live weight traits at specific or standardized ages, improving the data structure. Efforts to reallocate breeder males and females to new mates should also be stepped up, to ensure more male-female combinations to further improve the data structure. This would arguably further assist in the partitioning of variances.

Nonetheless, the substantial variation in growth, moderate to high heritability estimates and high and favourable genetic correlations amongst juvenile ostrich weight traits, indicate that genetic selection for improved slaughter weight at an early age is feasible. Since slaughter production and profitability is reliant on the various slaughter products (meat, leather and feathers), the relationship of these with slaughter weight must also be determined in order to formulate a selection index for slaughter birds. These aspects will be explored in the following chapters.

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CHAPTER 3

Environmental and genetic factors influencing quantitative ostrich slaughter and meat yield traits

3.1 Introduction

The commercial ostrich farming industry in South Africa originally developed as a result of the market for ostrich feathers (Shanawany, 1995; Smith, 1995; Sales, 1999). After the collapse of the feather market, the industry came to mainly rely on leather processed from the ostrich skins (Smith *et al.*, 1995). Ostrich meat was originally utilized in South Africa only for biltong (salted, dried meat) production (Osterhoff, 1979). The marketing of fresh meat has since grown to such an extent that ostrich meat has since become one of the main sources of income for the ostrich slaughter industry. This can in part be attributed to increased health awareness (Joy, 2005; Bingol & Ergun, 2011) and the increasing demand for alternative red meat sources after outbreaks of bovine spongiform encephalopathy (BSE) and foot and mouth disease among cattle in Europe (Hoffman, 2005; Polawska *et al.*, 2011). Ostrich meat is seen as a healthy red meat with a low fat and sodium content (Shanawany, 1995; Sales, 1996). When the meat is exported it can contribute up to 60% of slaughter income from individual birds, depending on the relative income from the other products.

The producer's income from meat is generally dependent on quantity, or yield, with the price per kilogram of carcass weight increasing non-linearly with an increase in size. In contrast to other species, where meat is sold as cuts or portions, the meat derived from ostriches is mostly sold as individual muscles (Sales & Horbanczuk, 1998; Hoffman, 2008). This highlights the importance of individual muscle yield in addition to carcass yield. The trade names of ostrich muscles are not standardized (Sales & Horbanczuk, 1998) however, and differ between countries (Mellett, 1995). Some of the first work conducted on the nomenclature and development of ostrich muscles was by Mellett (1985; 1992; 1994). Classification is usually based on the position of specific muscles, and it is known that certain characteristics differ between muscles (Sales, 1996; Cooper & Horbanczuk, 2002).

The highest percentage of usable meat in an ostrich carcass is situated on the legs and a lesser quantity is situated in the pair of muscles from the back (Sales, 1999). According to Mellett (1992), four additional products, namely the neck, liver, stomach and heart of ostriches are of economic importance. However, producers are currently only paid for the neck, which is weighed as part of the carcass and therefore included in carcass weight. The liver, stomach, heart and fat of the ostrich are removed as by-products during evisceration and do not form part of the carcass *per se*.

Abdominal and subcutaneous fat depots are generally regarded as the main sources of waste in chickens (Griffiths *et al.*, 1978; Becker *et al.*, 1981). However, due to being highly correlated with total carcass fat, abdominal fat is used as the main criterion reflecting excessive fat deposition in birds (Chambers, 1990). In ostriches, most of the fat is situated in the abdominal and subcutaneous depots, while intramuscular fat is below 0.5% (Mellett, 1992; Sales, 1999; Hoffman *et al.*, 2012). The problem of high intramuscular fatness affecting the nutritional characteristics of poultry meat is therefore not foreseen to be as problematic in ostriches.

Ratite fat is commonly utilized as oil in cosmetics and first-aid products (Sales, 1999; Hoffman, 2008; Hoffman *et al.*, 2012). In contrast to the emu industry, where fat is successfully utilized and marketed as valuable oil, the fat of ostriches is not utilized on a large scale at this stage and is mostly treated as a waste product - this despite of recent studies showing that emu and ostrich oils had similar properties due to their fatty acid composition (Bennett *et al.*, 2008).

Genetic improvement of carcass traits in other species has become an important tool at the disposal of producers specialising in meat production. Improving the yield of ostrich carcass components of economic importance also needs to be investigated in light of the importance of meat production for the ostrich industry. To establish a breeding program to improve carcass composition and yield in ostriches, it is essential to gain knowledge of the genetic parameters involving carcass traits. Since this is currently lacking, this study aimed to estimate genetic parameters for quantitative ostrich slaughter and meat traits. The relationships of these traits with body weight are also reported.

3.2 Materials and methods

3.2.1 Data description

Slaughter data were collected from the progeny of the commercial ostrich breeding flock maintained at the Oudtshoorn Research Farm, South Africa, slaughtered from 1997 to 2011. The management of the flock and their offspring are discussed in detail in Chapter 2.

Slaughter and meat data were matched with the on-farm records of each ostrich to link pedigree information to the data. The available data consisted of 3 656 records of slaughter ostriches from 119 to 5 388 days of age. Selection and treatment of slaughter groups was not standardized, however, resulting in large variation in slaughter age and weight across years and slaughter groups. Experimental slaughtering over years for different purposes, as well as the slaughtering of culled breeder ostriches contributed to the large variation. It was consequently decided to only use data from the South African Black ostriches slaughtered between 210 and 540 days of age for analyses. This age range was more representative of an acceptable range for industry slaughter birds.

Comparable live weight data from birds selected to become parents of subsequent generations from the same contemporary groups as the slaughtered ostriches were also added to the analyses. Contemporary groups for weight were defined as year by season to represent chicks that were reared in the same environment and management regime (see Chapter 2). Contemporary groups of less than 10 were pooled with adjacent contemporary groups where possible, or removed from the data where it could not be done sensibly, resulting in 32 contemporary groups for live weight. Slaughter date was used to derive contemporary groups for slaughter traits, thereby representing ostriches slaughtered under the same slaughter conditions. There were 37 slaughter groups after removal of slaughter groups of less than 10 ostriches.

The final dataset analysed represented 1 593 slaughter birds and 304 breeding birds (with comparable weight data), the progeny of 305 sires and 298 dams, mated to each other in 382 unique combinations.

Ostriches were weighed on the farm, either before pre-slaughter isolation (approximately 14 days before slaughter) or before transportation to the abattoir, to obtain a pre-slaughter live weight. The actual age at weighing was fitted in models. The ostriches were slaughtered and dressed at a local European Union approved ostrich abattoir, according to standard South African techniques as described by Wotton & Sparrey (2002), Brand (2006) and Hoffman (2012). The ostriches were fasted for 24 h, electrically stunned, hoisted by the legs and bled before the feathers, skins, internal organs and abdominal fat were removed. The carcasses were subsequently weighed, before excision of the pelvic limbs and removal of the necks. The raw skin size was also measured at the tannery.

Slaughter data routinely recorded at the abattoir included *post mortem* weight (after bleeding out) and warm carcass weight. For experimental purposes, the weights of various carcass components, including the raw skin, subcutaneous fat, neck, heart, liver and abdominal fat, were also determined for some of the slaughter groups. These weights are not routinely recorded by the abattoir for individual birds. Measurements could therefore unfortunately not be made for all birds slaughtered, resulting in varying numbers of records for these components.

A number of right pelvic limbs from various slaughter groups were removed from the abattoir 24 hours after slaughter for further dissection and investigation, assuming symmetrical distribution of muscle weight between pelvic limbs (Smith *et al.*, 2006). The weights of the pelvic limbs (leg and thigh) were determined after being chilled at 0°C for 24 h. Since the different muscles are sold as commercial cuts, ten of the major muscles were dissected and weighed. Trimming of the muscles was done by the same person throughout.

Using the comprehensive review by Sales (1999) as guidance, the scientific and USA trade names (Anon., 1996), of the muscles that were studied are given in Table 3.1. The muscles are grouped according to the anatomical classification as given by Mellett (1994). The location of these muscles on the pelvic limb is shown in Figure 3.1 and 3.2. The trade names of the respective muscles will be used subsequently for ease of reference.

Table 3.1 Scientific and trade names of different ostrich muscles used in this study

Anatomy / location	Trade name	Scientific name
Lower leg muscles / drum	Inside leg	<i>Muscularis gastrocnemius pars interna</i>
	Mid leg	<i>Muscularis fibularis longus</i>
	Outside leg	<i>Muscularis gastrocnemius pars externa</i>
Femoral muscles	Tip, trimmed	<i>Muscularis femorotibialis medius</i>
Post-acetabular muscles	Inside strip	<i>Muscularis iliofemoralis</i>
	Outside strip	<i>Muscularis flexor cruris lateralis</i>
	Fan	<i>Muscularis iliofibularis</i>
	Round	<i>Muscularis iliotibialis lateralis</i>
Acetabular muscles	Oyster	<i>Muscularis iliofemoralis externus</i>
Pre-acetabular muscles	Top loin	<i>Muscularis iliotibialis cranialis</i>

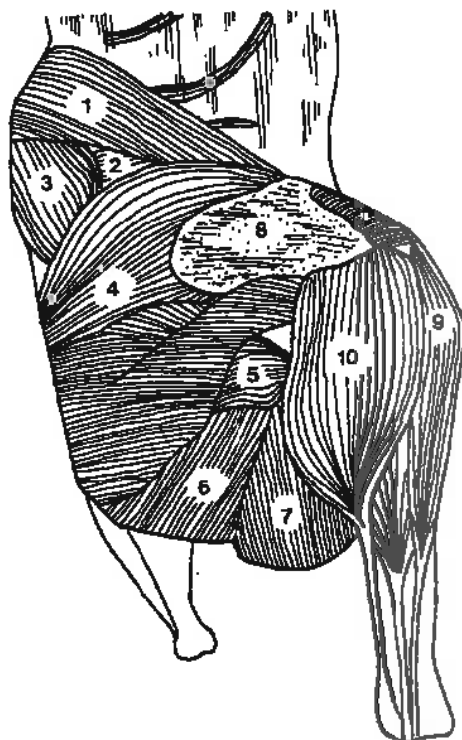


Figure 3.1 Muscles of the superficial layer of the pelvic limb of the ostrich, lateral view of the right leg. The muscles that were studied were: 1. *M. iliotibialis cranialis*; 3. *M. iliofemoralis externus*; 4. *M. iliotibialis lateralis*; 5. *M. iliofibularis*; 6. *M. flexor cruris lateralis*; 8. *M. femorotibialis medius*; 9. *M. fibularis longus*; 10. *M. gastrocnemius* (as reprinted from Mellett, 1994)

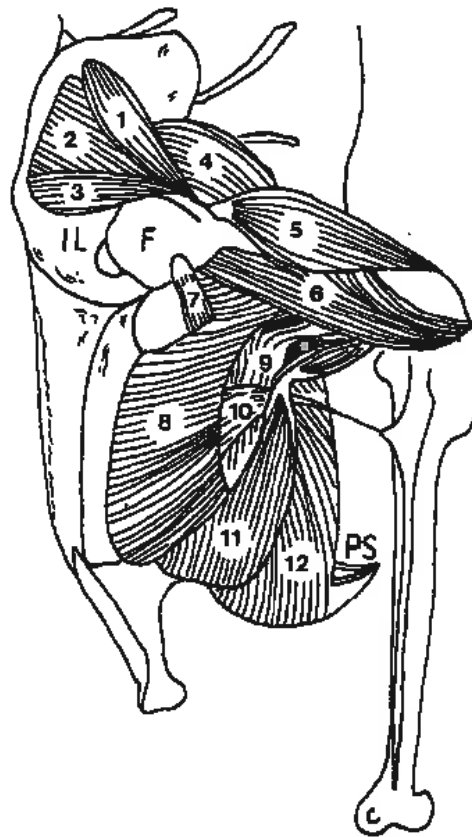


Figure 3.2 The third and fourth layers of muscles of the proximal part of the pelvic limb of the ostrich, showing the *M. iliofemoralis* (no. 8) that were studied (as reprinted from Mellett, 1994)

3.2.2 Statistical analysis

The data was analysed with a linear mixed animal model using ASReml (Gilmour *et al.*, 2009). Fixed effects fitted for all traits initially included contemporary group for live weight, slaughter group for slaughter traits and gender (male or female). Age was fitted as a linear covariate for all traits. Two-way interactions between these effects were also included in the initial models. Only effects found to be significant were fitted in the final models for each trait.

Variance components were estimated by REML procedures fitting an animal model. The full linear mixed model (in matrix notation) was:

$$y = X\beta + Z_1a + Z_2pe + e$$

where y was the vector of observations for the respective slaughter or meat traits; β , a and c were vectors of fixed effects, direct genetic (h^2) and maternal permanent environmental (pe^2) effects, respectively. X was an

incidence matrix relating records to the fixed effects (β), Z_1 and Z_2 were the corresponding incidence matrices relating the respective effects to y , while e was the vector of residuals.

It was assumed that:

$$\text{Var}(a) = A\sigma_a^2; \text{Var}(pe) = I\sigma_{pe}^2 \text{ and } \text{Var}(e) = I\sigma_e^2$$

where A was the numerator relationship matrix accounting for relationships among animals, I was an identity matrix and σ_a^2 , σ_{pe}^2 and σ_e^2 were the additive direct, permanent maternal environmental and residual variances, respectively.

Two random models were fitted. Model 1 only included the direct genetic effects, while the permanent maternal environmental effect was added in Model 2. This model choice was motivated by the results of Chapter 2, where it was evident that σ_{pe}^2 may still be important at slaughter age in ostriches in single-trait analyses. However, it also needs to be stated that these variances generally repartitioned to σ_a^2 when data were combined in multi-trait analyses involving meat traits. There were also no cases in which the random effect of hen within year was significant as for some weight traits in Chapter 2. Log-likelihood ratio tests were carried out to determine whether the permanent environmental effect contributed significantly to each trait.

Single-trait analyses were used to derive heritability estimates for live weight, carcass and meat traits. Subsequently, several multi-trait animal models, including groups of related traits, were fitted. These included models involving live weight and raw skin traits, carcass traits and groups of muscle weight traits, respectively. The three lower leg muscles were analysed together, as was the four post-acetabular muscles. The rest of the muscles (tip trimmed, oyster and top loin), which could not be conclusively grouped according to location, was analysed together.

Models used for each trait within the multi-trait analysis were those developed in single-trait analyses. These analyses allowed the calculation of all relevant correlations among traits, together with their respective standard errors.

Results from the multi-trait analyses were compared using the restricted maximum likelihood (REML) form of the Akaike's Information criterion (AIC), that imposes penalties according to the number of parameters to be estimated, and Schwarz' Bayesian Information criterion (BIC), which takes into account model uncertainty as well, and is stricter than the AIC (Huisman *et al.*, 2002).

All analyses included the full pedigree file, consisting of 6 541 individuals, the progeny of 378 sires and 376 dams, mated to each other in 541 unique combinations. Individuals hatched from generation one through seven were included.

3.3 Results

3.3.1 Descriptive statistics

Means and standard deviations for the respective live weight and slaughter traits are presented in Table 3.2. The average slaughter age was 373 ± 76 days. Due to the inconsistent recording of specific data, the number of observations (N) varied significantly among traits. Abdominal and subcutaneous fat weights were highly variable as reflected by high coefficients of variation of >50%, while coefficients of variation in the other traits were between 12 and 29%.

Table 3.2 Means (\pm s.d.), coefficients of variation (CV) and ranges for ostrich slaughter and meat traits

Trait	N	Mean (\pm s.d.)	CV (%)	Range
<u>Slaughter traits:</u>				
Live weight (kg)	1 897	90.3 \pm 19.3	21	42 - 146
<i>Post mortem</i> weight (kg)	1 052	84.2 \pm 13.1	16	43.5 - 134.7
<u>Raw skin traits:</u>				
Raw skin size (dm ²)	1 134	128 \pm 15	12	82 - 158
Raw skin weight (kg)	754	4.620 \pm 1.287	28	2.014 - 7.616
<u>Carcass traits:</u>				
Carcass weight (kg)	1 268	41.8 \pm 7.3	17	20.1 - 62.7
Pelvic limb weight (kg)	976	14.8 \pm 3.0	20	6.5 - 23.4
Abdominal fat weight (kg)	424	3.708 \pm 2.035	55	0.238 - 10.220
Subcutaneous fat weight (kg)	737	2.687 \pm 1.593	59	0.293 - 10.166
<u>Carcass component traits:</u>				
Neck weight (kg)	648	1.545 \pm 0.317	21	0.789 - 2.485
Liver weight (kg)	611	1.493 \pm 0.338	23	0.683 - 2.551
Heart weight (kg)	610	0.795 \pm 0.182	23	0.333 - 1.319
<u>Quantitative meat traits:</u>				
Inside leg weight (kg)	738	0.793 \pm 0.191	24	0.284 - 1.446
Mid leg weight (kg)	738	0.263 \pm 0.067	25	0.102 - 0.487
Outside leg weight (kg)	738	0.527 \pm 0.150	28	0.192 - 1.157
Round weight (kg)	740	0.988 \pm 0.230	23	0.268 - 1.560
Fan weight (kg)	871	1.394 \pm 0.339	24	0.368 - 2.400
Inside strip weight (kg)	775	0.357 \pm 0.102	29	0.105 - 0.637
Outside strip weight (kg)	740	0.285 \pm 0.083	29	0.103 - 0.531
Top loin weight (kg)	739	0.445 \pm 0.109	24	0.171 - 0.852
Oyster weight (kg)	740	0.168 \pm 0.039	23	0.077 - 0.289
Tip, trimmed weight (kg)	739	0.659 \pm 0.136	21	0.312 - 1.171

N: number of records; s.d.: standard deviation; CV: coefficient of variation

3.3.2 Fixed effects

All the traits under consideration were dependent on age (with the exception of *post mortem* weight, inside strip weight and liver weight) and contemporary group (Table 3.3). The interaction of age and contemporary group was also significant for most of the traits, suggesting that age effects were not consistent for all contemporary groups. For instance, regressions of live weight on age by contemporary group ranged from -0.807 ± 0.361 kg/day (for chicks hatched in late summer of 2001) to 0.790 ± 0.526 kg/day (for chicks hatched during early summer in 1997). The size of the contemporary groups varied appreciably, from 15 (1997) to 66 (2001) in the before-mentioned example, which may have contributed to the difference in regressions.

Table 3.3 Significant^a fixed effects influencing ostrich slaughter and meat traits

Trait	Age	Contemporary group (CG)	Gender (G)	Age x CG	Age x G	G x CG	R ²
<u>Slaughter traits:</u>							
Live weight ^b	***	***	n.s.	***	n.s.	n.s.	0.67
<i>Post mortem</i> weight	n.s.	***	n.s.	n.s.	n.s.	n.s.	0.40
<u>Raw skin traits:</u>							
Raw skin size	***	***	n.s.	***	n.s.	n.s.	0.70
Raw skin weight	**	***	***	***	**	**	0.72
<u>Carcass traits:</u>							
Carcass weight	**	***	*	***	n.s.	n.s.	0.48
Pelvic limb weight	***	***	n.s.	***	n.s.	n.s.	0.63
Abdominal fat weight	**	***	***	**	n.s.	n.s.	0.61
Subcutaneous fat weight	**	***	**	*	**	n.s.	0.36
<u>Carcass component traits:</u>							
Neck weight	*	***	***	***	n.s.	n.s.	0.63
Liver weight	n.s.	***	n.s.	n.s.	n.s.	n.s.	0.64
Heart weight	***	***	n.s.	***	n.s.	n.s.	0.63
<u>Quantitative meat traits:</u>							
Inside leg weight	***	***	n.s.	***	*	n.s.	0.53
Mid leg weight	**	***	n.s.	***	n.s.	n.s.	0.49
Outside leg weight	***	***	n.s.	***	n.s.	*	0.54
Round weight	***	***	n.s.	***	n.s.	n.s.	0.53
Fan weight	***	***	*	***	n.s.	n.s.	0.64
Inside strip weight	n.s.	***	n.s.	***	*	n.s.	0.55
Outside strip weight	***	***	n.s.	***	n.s.	n.s.	0.44
Top loin weight	***	***	n.s.	***	n.s.	n.s.	0.53
Oyster weight	***	***	**	***	n.s.	n.s.	0.47
Tip, trimmed weight	**	***	***	*	n.s.	n.s.	0.40

^a Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s.: not significant

^b For live weight, age refers to age at last live weighing and contemporary group refers to rearing group, while for the rest of the traits, age refers to slaughter age and contemporary group to slaughter group

Gender influenced raw skin weight, neck weight and fat weight, as well as some of the muscle weights. Least square means for traits affected by gender are reported in Table 3.4.

Table 3.4 Least square means (\pm s.e.) for slaughter and meat traits of ostriches influenced by gender

Trait	Male	Female
Skin weight (kg)	1.52 \pm 0.02	1.72 \pm 0.02
Abdominal fat (kg)	3.943 \pm 0.062	4.431 \pm 0.062
Subcutaneous fat (kg)	2.472 \pm 0.047	2.750 \pm 0.047
Neck weight (kg)	0.971 \pm 0.008	0.917 \pm 0.008
Fan weight (kg)	1.371 \pm 0.007	1.400 \pm 0.007
Oyster weight (kg)	0.190 \pm 0.001	0.183 \pm 0.001
Tip, trimmed weight (kg)	0.671 \pm 0.004	0.699 \pm 0.004

Males generally had lighter skins than females, and less fat than females (3.9 vs. 4.4 kg abdominal fat and 2.5 vs. 2.7 kg subcutaneous fat). Males had heavier necks than females.

The effect of gender on muscle weights was inconsistent, with males having heavier oyster cuts and females having heavier fan and tip, trimmed weights. Significant differences between muscle weights were small in absolute terms, however, ranging between 2.1 and 4.1% of the lower mean weight.

3.3.3 (Co)variance components, ratios and correlations

3.3.3.1 Single-trait results

The inclusion of the direct genetic component as a random effect in the operational model resulted in an improved log-likelihood for all traits, with the exception of liver and abdominal fat weight (Table 3.5). The inclusion of the maternal permanent environmental effect in the operational model resulted in an improved log-likelihood for live weight, pelvic limb weight, neck weight, subcutaneous fat weight and some of the muscle weights.

Although not significant for all traits, the direct genetic component was fitted as default for all traits, resulting in heritability estimates (h^2) of between 0.09 (abdominal fat weight) and 0.44 (*post mortem* weight) for the respective slaughter and meat traits in single-trait analyses (Table 3.6). Some heritability estimates were not significant though, as reflected by standard errors exceeding half of the corresponding estimate.

Significant heritability estimates of 0.33 were obtained for fan and oyster weight, while the heritability estimates for carcass weight and neck weight were the only significant estimates for the carcass component traits.

Maternal permanent environmental variance ratios (pe^2) accounted for between 5% (live weight) and 17% (neck weight) of the phenotypic variation for the respective traits (Table 3.6).

Table 3.5 Log-likelihood (LogL) values for models^a fitting different random effects for ostrich slaughter and meat traits in single-trait animal model analysis. The best model is denoted in bold.

Trait	Model		
	FE	FE + h ²	FE + h ² + pe ²
<u>Slaughter traits:</u>			
Live weight	-5541.49	-5457.09	-5454.26
<i>Post mortem</i> weight	-2918.56	-2876.55	-2875.28
<u>Skin traits:</u>			
Raw skin size	-3292.10	-3251.06	-3250.51
Raw skin weight	-244.201	-209.700	-209.619
<u>Carcass traits:</u>			
Carcass weight	-2788.42	-2753.52	-2753.44
Pelvic limb weight	-1200.29	-1176.65	-1174.08
Abdominal fat weight	-387.298	-386.873	-386.132
Subcutaneous fat weight	-565.552	-548.553	-545.808
<u>Carcass component traits:</u>			
Neck weight	555.652	566.332	569.042
Liver weight	609.538	610.987	612.017
Heart weight	842.904	851.245	851.245
<u>Quantitative meat traits:</u>			
Inside leg weight	891.110	901.188	906.419
Mid leg weight	1569.54	1574.56	1575.57
Outside leg weight	984.445	988.453	989.509
Round weight	761.639	779.926	782.685
Fan weight	709.617	726.125	728.621
Inside strip weight	1396.47	1403.71	1405.39
Outside strip weight	1401.58	1406.32	1406.90
Top loin weight	1267.96	1275.79	1276.01
Oyster weight	1929.45	1943.32	1943.43
Tip, trimmed weight	1035.94	1048.69	1050.29

^a FE: fixed effects only; h²: animal genetic effect; pe²: maternal permanent environmental effect

Table 3.6 (Co)variance components and ratios^a (\pm s.e.) for ostrich slaughter and meat traits estimated from single-trait analyses

Trait	h^2	pe^2	σ^2_a	σ^2_{pe}	σ^2_e	σ^2_p
<u>Slaughter traits:</u>						
Live weight	0.21 \pm 0.06	0.05 \pm 0.03	26.2	6.76	91.3	124.3
<i>Post mortem</i> weight	0.44 \pm 0.08		44.8		58.0	102.8
<u>Skin traits:</u>						
Raw skin size	0.31 \pm 0.07		19.4		43.9	63.3
Raw skin weight	0.39 \pm 0.10		0.180		0.286	0.466
<u>Carcass traits:</u>						
Carcass weight	0.29 \pm 0.06		7.9		19.6	27.5
Pelvic limb weight	0.18 \pm 0.09	0.08 \pm 0.04	0.601	0.280	2.552	3.433
Abdominal fat weight	0.09 \pm 0.09		0.140		1.484	1.624
Subcutaneous fat weight	0.16 \pm 0.12	0.14 \pm 0.06	0.257	0.222	1.150	1.628
<u>Carcass component traits:</u>						
Neck weight	0.02 \pm 0.10	0.17 \pm 0.07	0.001	0.007	0.030	0.038
Liver weight	0.11 \pm 0.07		0.005		0.037	0.042
Heart weight	0.23 \pm 0.09		0.003		0.009	0.012
<u>Quantitative meat traits:</u>						
Inside leg weight	0.07 \pm 0.09	0.16 \pm 0.06	0.001	0.003	0.013	0.017
Mid leg weight	0.16 \pm 0.08		0.000		0.002	0.002
Outside leg weight	0.17 \pm 0.08		0.002		0.009	0.010
Round weight	0.20 \pm 0.11	0.10 \pm 0.05	0.005	0.003	0.017	0.025
Fan weight	0.33 \pm 0.09	0.10 \pm 0.05	0.006	0.014	0.031	0.042
Inside strip weight	0.16 \pm 0.07		0.001		0.004	0.005
Outside strip weight	0.21 \pm 0.08		0.001		0.003	0.004
Top loin weight	0.21 \pm 0.08		0.001		0.005	0.006
Oyster weight	0.33 \pm 0.10		0.000		0.001	0.001
Tip, trimmed weight	0.30 \pm 0.09		0.003		0.008	0.011

^a h^2 : direct heritability; pe^2 : maternal permanent environmental effect; σ^2_a : direct additive variance; σ^2_{pe} : maternal permanent environmental variance; σ^2_e : residual variance; σ^2_p : total phenotypic variance

3.3.3.2 Multi-trait results

The maternal permanent environmental effect for all traits became insignificant in multi-trait analysis (as reflected by log-likelihood values, AIC and/or BIC values) and was subsequently not included in the final analysis involving any combination of traits.

The genetic correlation between live weight and *post mortem* weight amounted to 0.99 ± 0.01 in a two-trait analysis involving these traits. It was therefore decided to use live weight for all subsequent analyses, since live weight records were available for parents as well, while *post mortem* weight was only recorded in

individuals that were slaughtered. There were also less records available for *post mortem* weight than for live weight.

3.3.3.2.1 Raw skin traits

Results from a three-trait model including live weight and raw skin traits are given in Table 3.7.

Table 3.7 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations between ostrich slaughter and raw skin traits from a three-trait analysis

Trait	Live weight	Raw skin size	Raw skin weight
<i>Additive genetic correlations (h^2 in bold)</i>			
Live weight	0.44 \pm 0.07	0.90 \pm 0.03	0.89 \pm 0.04
Raw skin size		0.38 \pm 0.07	0.85 \pm 0.06
Raw skin weight			0.42 \pm 0.08
<i>Residual correlations (σ^2_e in bold)</i>			
Live weight	106	0.80 \pm 0.02	0.71 \pm 0.04
Raw skin size		52.5	0.68 \pm 0.04
Raw skin weight			0.389
<i>Phenotypic correlations (σ^2_p in bold)</i>			
Live weight	188	0.84 \pm 0.01	0.79 \pm 0.02
Raw skin size		84.1	0.75 \pm 0.02
Raw skin weight			0.669

Estimates of heritability (h^2) were moderate to high for all three traits. Live weight was genetically highly correlated with both raw skin size and skin weight, while the genetic correlation between skin size and skin weight was also high. Residual and phenotypic correlations were somewhat lower, but still comparable to genetic correlations in sign and magnitude.

3.3.3.2.2 Carcass traits

Results from a five-trait model including live weight and various carcass component traits are given in Table 3.8. All heritability estimates were moderate. The major difference from the results in Table 3.8 compared to the single-trait analyses in Table 3.6, is the lack of dam permanent environmental variance components, contributing to higher heritability estimates reported for all traits involved in the five-trait analysis. Genetic correlations were very high between live weight and carcass weight, as well as between live weight and pelvic limb weight. Carcass weight and pelvic limb weight were also highly correlated, the derived genetic correlation not differing from unity.

A high genetic correlation was also found between live weight and subcutaneous fat weight, while correlations of weight traits were lower with abdominal fat weight. The residual and phenotypic correlations between the weight traits and abdominal fat were mostly higher than those with subcutaneous fat weight though. The genetic correlation between abdominal fat weight and subcutaneous fat weight amounted to 0.63, with the 95% confidence interval for the correlation (0.27 - 0.99) just excluding unity. Residual and phenotypic correlations were comparable to genetic correlations in sign, but in some cases somewhat smaller or larger in absolute magnitude.

Table 3.8 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations between ostrich live weight and carcass traits from multi-trait analyses

Trait	Live weight	Carcass weight	Pelvic limb weight	Abdominal fat weight	Subcutaneous fat weight
<i>Additive genetic correlations (h^2 in bold)</i>					
Live weight	0.34 \pm 0.06	0.94 \pm 0.03	0.90 \pm 0.04	0.56 \pm 0.16	0.92 \pm 0.07
Carcass weight		0.27 \pm 0.06	0.99 \pm 0.01	0.47 \pm 0.18	0.73 \pm 0.12
Pelvic limb weight			0.32 \pm 0.06	0.41 \pm 0.19	0.67 \pm 0.13
Abdominal fat weight				0.22 \pm 0.08	0.63 \pm 0.18
Subcutaneous fat weight					0.21 \pm 0.06
<i>Residual correlations (σ_e^2 in bold)</i>					
Live weight	81	0.71 \pm 0.02	0.75 \pm 0.02	0.62 \pm 0.05	0.52 \pm 0.04
Carcass weight		21.6	0.93 \pm 0.01	0.62 \pm 0.05	0.38 \pm 0.05
Pelvic limb weight			2.68	0.54 \pm 0.06	0.34 \pm 0.05
Abdominal fat weight				1.5	0.48 \pm 0.05
Subcutaneous fat weight					1.3
<i>Phenotypic correlations (σ_p^2 in bold)</i>					
Live weight	123	0.78 \pm 0.01	0.80 \pm 0.01	0.60 \pm 0.03	0.62 \pm 0.02
Carcass weight		29.7	0.94 \pm 0.00	0.58 \pm 0.03	0.46 \pm 0.03
Pelvic limb weight			3.9	0.50 \pm 0.03	0.42 \pm 0.03
Abdominal fat weight				1.9	0.63 \pm 0.03
Subcutaneous fat weight					1.7

3.3.3.2.3 Carcass component traits

Results from a four-trait model including live weight and various carcass component traits are given in Table 3.9. The heritability estimate of liver weight was not significant (as in Table 3.6), while moderate heritability estimates were obtained for neck weight and heart weight. The higher heritability of neck weight in Table 3.9, where the dam permanent environmental variance was not significant, compared to the estimate in Table 3.6 is notable.

The genetic correlations of live weight with these components ranged in the medium to high range from 0.53 to 0.64, and were consistently larger than twice the corresponding standard error. The genetic correlations among neck, liver and heart weights were not very high though, at levels below the corresponding standard errors. Whereas phenotypic and residual correlations involving live weight were comparable in magnitude to genetic correlations, this generalisation did not seem to apply to correlations among neck, liver and heart weights. Phenotypic and residual correlations were generally larger in magnitude than genetic correlations when correlations among neck, liver and heart weights were involved.

Table 3.9 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations between ostrich live weight and carcass component traits from multi-trait analyses

Trait	Live weight	Neck weight	Liver weight	Heart weight
<i>Additive genetic correlations (h^2 in bold)</i>				
Live weight	0.33 \pm 0.06	0.59 \pm 0.11	0.64 \pm 0.23	0.53 \pm 0.16
Neck weight		0.45 \pm 0.09	0.18 \pm 0.30	0.12 \pm 0.20
Liver weight			0.08 \pm 0.06	-0.09 \pm 0.35
Heart weight				0.26 \pm 0.08
<i>Residual correlations (σ_e^2 in bold)</i>				
Live weight	91	0.67 \pm 0.05	0.51 \pm 0.05	0.60 \pm 0.05
Neck weight		0.026	0.38 \pm 0.07	0.65 \pm 0.07
Liver weight			0.040	0.50 \pm 0.06
Heart weight				0.010
<i>Phenotypic correlations (σ_p^2 in bold)</i>				
Live weight	137	0.63 \pm 0.03	0.50 \pm 0.03	0.58 \pm 0.03
Neck weight		0.047	0.30 \pm 0.04	0.46 \pm 0.04
Liver weight			0.044	0.40 \pm 0.04
Heart weight				0.014

3.3.3.2.4 Meat yield traits

Results from multi-trait models including live weight and various economically important muscles are given in Tables 3.10, 3.11 and 3.12, based on the grouping of muscles as explained earlier.

Heritability estimates were low to moderate, but significant for all traits. The estimates were mostly of similar range to those obtained in single-trait analyses, or higher.

The genetic correlations between live weight and the individual muscle weights ranged from moderate to very high at 0.59 to 0.82 and were all positive and significant. Corresponding ranges amounted to 0.46 to 0.73 for residual correlations and 0.53 to 0.72 for phenotypic correlations.

Genetic correlations among specific muscle weights within groups ranged from moderate to very high, amounting to between 0.45 and 0.99. Corresponding ranges amounted to between 0.16 and 0.64 for residual correlations and between 0.46 and 0.76 for phenotypic correlations.

Table 3.10 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations between ostrich live weight and lower leg muscle weights from multi-trait analyses

Trait	Live weight	Inside leg	Mid leg	Outside leg
<i>Additive genetic correlations (h^2 in bold)</i>				
Live weight	0.34 \pm 0.06	0.62 \pm 0.12	0.75 \pm 0.12	0.76 \pm 0.13
Inside leg		0.29 \pm 0.08	0.84 \pm 0.11	0.84 \pm 0.13
Mid leg			0.22 \pm 0.07	0.99 \pm 0.12
Outside leg				0.14 \pm 0.06
<i>Residual correlations (σ^2_e in bold)</i>				
Live weight	90	0.72 \pm 0.04	0.46 \pm 0.05	0.58 \pm 0.04
Inside leg		0.014	0.51 \pm 0.05	0.60 \pm 0.04
Mid leg			0.002	0.47 \pm 0.05
Outside leg				0.010
<i>Phenotypic correlations (σ^2_p in bold)</i>				
Live weight	137	0.67 \pm 0.02	0.53 \pm 0.03	0.60 \pm 0.03
Inside leg		0.020	0.59 \pm 0.03	0.64 \pm 0.02
Mid leg			0.003	0.56 \pm 0.03
Outside leg				0.011

Table 3.11 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations between ostrich live weight and post-acetabular muscle weights from multi-trait analyses

Trait	Live weight	Round	Fan	Inside strip	Outside strip
<i>Additive genetic correlations (h^2 in bold)</i>					
Live weight	0.34 \pm 0.06	0.69 \pm 0.09	0.71 \pm 0.09	0.59 \pm 0.15	0.65 \pm 0.13
Round		0.43 \pm 0.09	0.72 \pm 0.09	0.55 \pm 0.16	0.76 \pm 0.11
Fan			0.33 \pm 0.08	0.65 \pm 0.15	0.71 \pm 0.13
Inside strip				0.19 \pm 0.07	0.52 \pm 0.20
Outside strip					0.23 \pm 0.07
<i>Residual correlations (σ_e^2 in bold)</i>					
Live weight	90	0.66 \pm 0.05	0.73 \pm 0.03	0.55 \pm 0.05	0.50 \pm 0.05
Round		0.018	0.80 \pm 0.04	0.59 \pm 0.05	0.52 \pm 0.05
Fan			0.034	0.62 \pm 0.04	0.54 \pm 0.05
Inside strip				0.004	0.16 \pm 0.02
Outside strip					0.003
<i>Phenotypic correlations (σ_p^2 in bold)</i>					
Live weight	137	0.67 \pm 0.02	0.72 \pm 0.02	0.55 \pm 0.03	0.54 \pm 0.03
Round		0.031	0.76 \pm 0.02	0.56 \pm 0.03	0.58 \pm 0.03
Fan			0.051	0.62 \pm 0.03	0.59 \pm 0.03
Inside strip				0.005	0.46 \pm 0.03
Outside strip					0.004

Table 3.12 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations between ostrich live weight and muscle weights from multi-trait analyses

Trait	Live weight	Top loin	Oyster	Tip, trimmed
<i>Additive genetic correlations (h^2 in bold)</i>				
Live weight	0.34 \pm 0.06	0.73 \pm 0.11	0.80 \pm 0.10	0.82 \pm 0.08
Top loin		0.19 \pm 0.07	0.45 \pm 0.18	0.78 \pm 0.12
Oyster			0.26 \pm 0.07	0.47 \pm 0.16
Tip, trimmed				0.32 \pm 0.08
<i>Residual correlations (σ^2_e in bold)</i>				
Live weight	91	0.61 \pm 0.04	0.53 \pm 0.05	0.59 \pm 0.04
Top loin		0.006	0.64 \pm 0.04	0.58 \pm 0.04
Oyster			0.001	0.60 \pm 0.05
Tip, trimmed				0.009
<i>Phenotypic correlations (σ^2_p in bold)</i>				
Live weight	137	0.63 \pm 0.02	0.61 \pm 0.03	0.67 \pm 0.02
Top loin		0.007	0.59 \pm 0.03	0.62 \pm 0.02
Oyster			0.001	0.56 \pm 0.03
Tip, trimmed				0.013

3.4 Discussion

3.4.1 Descriptive statistics

The coefficients of variation for body weight and skin traits were consistent with earlier reports (Bunter *et al.*, 1999; Bunter & Cloete, 2004; Engelbrecht *et al.*, 2005). Coefficients of variation for live weight and slaughter traits previously reported were generally between 10 and 25% (Cloete *et al.*, 2008), depending on the age range of the data used. Means for pre-slaughter live weight reported by Bunter *et al.* (1999), Bunter & Cloete (2004), Brand (2006) and Engelbrecht *et al.* (2005; 2007; 2009) ranged between 80.4 and 111.1 kg and standard deviations ranged from 9.2 to 21.7 kg. Means decreased and standard deviations increased as the age range increased. A similar mean raw skin size of 129.7 ± 14.1 dm², with a coefficient of variation of 10.9%, was reported by Engelbrecht *et al.* (2005), for a smaller subset of the data used during this study.

It was difficult to compare means for the carcass component weights with previous studies on ostriches noted in the literature due to considerable differences in weights reported for carcass components (Sales, 1999). This could be ascribed to differences in slaughter procedures, cutting methods, amount of trimming and varying carcass standards used in the industry (Sales & Horbanczuk, 1998; Sales, 1999). Furthermore, the genotype studied was frequently not mentioned, while indications are that there are differences between genotypes with regard to some carcass traits (Sales, 1999; Brand, 2006; Hoffman, 2008). However, values

of similar range were reported for carcass component weights and for muscle weights of similarly aged ostriches (Morris *et al.*, 1995; Sales, 1996).

The coefficient of variation for carcass weight was in the same range as those reported for carcass weights of sheep (14-18%, Greeff *et al.*, 2008), and slightly higher than reported for cattle (11%, Boukha *et al.*, 2011) and Japanese quail (11%, Lotfi *et al.*, 2011). The coefficient of variation for the carcass weight of a small group of similarly aged South African Black ostriches (n = 34) studied by Brand (2006) were 12%, while the coefficients of variation for muscle weights ranged from 11 to 16%.

The coefficients of variation for fat traits were approximately double that of muscle traits, which was in accordance with what was reported by Greeff *et al.* (2008) on Merino sheep and by Lotfi *et al.* (2011) for Japanese quail.

3.4.2 Fixed effects

Most carcass and meat traits were dependent on age, with yield generally increasing with an increased slaughter age, albeit that the regressions on age differed for respective contemporary groups. This finding is consistent with results reported by Mellett (1992), Sales (1994) and Brand *et al.* (2010). Girolami *et al.* (2003) also reported a significant age effect for pelvic limb weight, with generally higher regression coefficients for younger animals. This indicated that a decreased age at slaughter may affect production costs, through a shortened production cycle and improved production efficiency.

Gender seemed to influence skin and fat weights, with the raw skins of males being lighter than those of female ostriches. Males also had less fat, both in the abdominal and subcutaneous depots. It could be argued that the subcutaneous fat influenced raw skin weight, despite of the excess fat being trimmed off, thereby resulting in the female skins being heavier. Broiler males were also shown to be leaner than females (Zerehdaran *et al.*, 2004).

With regard to individual muscle weights, some muscles were heavier in females, while some were heavier in males. Carcass composition therefore seemed to differ slightly between male and females. This result would be consistent with studies on chickens, which showed that female chickens had a higher breast yield, but lower thigh and drumstick yields than males (Baeza *et al.*, 2010). Female chickens also had higher carcass fatness than males (Becker *et al.*, 1981), with the difference increasing with age. Previously, gender effects for ostrich live weights and slaughter traits were rarely found to be significant (Cloete *et al.*, 1998; Van Schalkwyk *et al.*, 2000; Cloete *et al.*, 2002; Kurtenkov, 2008). Cloete *et al.* (1998) reported that females produced the same drumstick weight and skin area as males, which is in agreement to the results reported here. It seems, however, that the contribution of different muscles to the thigh and leg may vary between males and females. Morris *et al.* (1995) also reported that females tended to have a slightly higher percentage of fat than males, but indicated that sex had no significant effect on slaughter and meat yields.

3.4.3 (Co)variance components, ratios and correlations

All carcass components, with the exception of the weight of the liver, showed significant genetic variation in multi-trait analyses, while no significant maternal permanent environmental effect was evident for ostrich carcass and meat traits in multi-trait analyses. These results are consistent with those reported in Chapter 2 and reinforce the contention that information supplied by other traits included in these analyses allows the repartitioning of variances away from maternal permanent environmental effects to direct additive effects.

Heritability estimates for live weight and skin traits were consistent with previous estimates reported by Bunter *et al.* (1999), Bunter & Cloete (2004) and Engelbrecht *et al.* (2005, 2007). The estimates from multi-trait analyses were generally slightly higher compared to single-trait estimates. Heritability estimates were comparable to estimates for other species. Lofti *et al.* (2011), for instance, reported heritability estimates of 0.59 for carcass weight, 0.32 for skin weight and 0.28 for abdominal fat weight of Japanese quail.

The heritability estimate for abdominal fat was lower than the estimate for broilers reported by Zerehdaran *et al.* (2004), presumably as a result of the low number of records.

The only other genetic parameters for ostrich slaughter and meat traits that could be found in the literature (Rosa *et al.*, 2011) were heritability estimates of 0.05, 0.20 and 0.05 for pre-slaughter live weight, carcass weight and carcass dressing percentage, respectively. These authors also reported a genetic correlation of 0.64 between carcass weight and live weight at 360 days. This estimate is appreciably lower than the correlation of 0.94 between pre-slaughter live weight and carcass weight found in the present study. However, the study of Rosa *et al.* (2011) was based on data from various genotypes, which could have contributed to the lower correlation reported.

Pre-slaughter live weight was highly correlated with carcass weight and pelvic limb weight. Unfortunately the genetic correlation between live weight and subcutaneous fat was also very high; indicating that selection for increased live weight and slaughter yield will increase the subcutaneous fat weight as well. If this fat can be exploited as a valuable oil, as is done in other ratite species (Sales, 1999; Sales, 2007; Bennett *et al.*, 2008), this could be beneficial though. The possible uses of ostrich fat should therefore be investigated further.

Lower genetic correlations were found between live weight and other carcass components, such as liver, heart and neck weights, although these correlations were still positive and higher than 0.50. These correlations were also accompanied by higher standard errors, presumably because of a lower number of records ($N < 650$) in some of these traits.

Moderate to high heritability estimates were found for most of the individual muscles, with a range from 0.14 to 0.43, while the genetic correlations between these individual muscle weights and pre-slaughter live weight were all positive and ranged from 0.59 to 0.82. Accordingly, genetic correlations among the weights of the respective muscles were also positive and ranged from between 0.54 and 0.99. No results to compare these

estimates with were found in the literature. However, since all genetic correlations among traits were favourable and in the medium to very high range, it is not expected that a selection index based on slaughter traits will be complicated by unwanted unfavourable genetic correlations.

This level of heritability estimates indicates that genetic improvement in ostrich carcass traits is achievable, as is expected for heritable and variable traits. Based upon the higher coefficients of variation for fat traits compared to that of muscle traits, as well as comparable heritability estimates, it could be contended that the change from selection would be considerably slower in muscle yield than in fat yield, under similar selection intensities. A similar conclusion was arrived at by Greeff *et al.* (2008), based on their analysis of sheep data.

3.5 Conclusions

The study provides genetic parameter estimates of quantitative meat traits that are needed to guide the development of a selection index for improved slaughter bird production. It has been demonstrated that sufficient genetic variation exists in most of the traits considered, thus facilitating the design of a specific breeding program. The estimated genetic relationships are mostly favourable, with a few exceptions, namely those involving fat depots. Since fat deposition is energetically a more intensive process, these correlations are seen as being undesirable unless a greater economic value can be negotiated for ostrich fat. Unlike the local ostrich industry, where fat is regarded as a waste product that needs to be disposed of, the fat of emus is considered as a valuable commodity of primary importance in the slaughter industry. The utilisation of ostrich fat in a similar fashion should therefore be investigated.

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CHAPTER 4

Environmental and genetic factors influencing ostrich meat quality traits

4.1 Introduction

Most of the meat from the commercial production of ostriches in South Africa is exported, with exports being dependent on the disease status of the exporting country. The 2011 outbreak of highly pathogenic notifiable avian influenza H5N2 in South Africa resulted in a ban of fresh meat exports, which has not yet been lifted, due to continuing virus activity. So, although ostrich meat income is directly dependent on quantity, with producers being compensated per kilogram of carcass weight, the quality and safety of the meat is of critical importance as pertaining to the marketing and consumption of the meat.

The ban on exports of fresh meat has led the local ostrich industry to increasingly focus on the export of heat-treated processed meat products (Hoffman, 2008). These new trends (*sous vide*) involve new demands in terms of the quality of the meat and specifically underline the importance of the technological quality of the meat. Le Bihan-Duval (2004) describes the technological quality of meat as its ability to be stored in the form of chopped meat or to be transformed into further-processed products. According to Le Bihan-Duval (2004) the rate and extent of *rigor mortis* development affects the technological quality of meat. Other histological, biophysical and physical characteristics of meat that are correlated with general meat quality, include fibre diameter, sarcomere length, collagen content, chemical composition, pH, cooking loss, shear force and pigment content (Sales, 1999).

Ostrich meat can be classified as an intermediate type red meat, i.e. with a pH between normal (<5.8) and extreme (>6.2), as measured 24 hours post-slaughter (Sales, 1996; Hoffman *et al.*, 2012). Meat with such a pH has a high water-holding capacity, which makes ostrich meat ideal for processing and the production of processed products (Sales & Mellett, 1996; Hoffman, 2008). The rate of pH decline after slaughter and the ultimate pH influences meat quality to a large extent (Sales & Mellett, 1996; Hoffman *et al.*, 2007), and has also been associated with attributes such as colour, tenderness, juiciness and microbial stability and shelf-life (Lawrie, 1998; Le Bihan-Duval, 2004). The colour of meat is important because it strongly affects consumers' choices as the first attribute detected and the most obvious visible characteristic of meat (Sales & Oliver-Lyons, 1996).

According to Le Bihan-Duval (2004), the quality of meat results from complex interactions between the genotype of the animal and its environment, in particular the stresses undergone before slaughter such as transport and lairage (Hoffman *et al.*, 2012). Various authors have reported the effects of environmental

factors on ostrich meat quality, including extrinsic and intrinsic factors, as reviewed by Sales & Oliver-Lyons (1996) and Hoffman (2005). Conversely, genetic variation in ostrich meat quality has received little attention to date. The genetic basis of meat quality has led to the inclusion of meat quality traits in selection indices applied in the pig industry, and it has more recently also found application in the poultry industry (Le Bihan-Duval, 2004). However, it has not been considered for the ostrich industry yet, with ostrich meat production being mostly quantitative at this stage, with little emphasis on qualitative traits.

It is therefore important to obtain the first estimates of heritability for ostrich meat quality traits and of their genetic correlations with other traits of economic importance in order to specify the possibilities of selection for these traits. This study consequently aims to estimate genetic parameters for ostrich meat quality traits, using measurements on the most valuable ostrich muscle, namely the *Muscularis iliofibularis*, also known as the fan fillet.

4.2 Materials and methods

4.2.1 Data description

Slaughter and meat data were collected from ostriches slaughtered between 1997 and 2011 from the progeny of the commercial ostrich breeding flock maintained at the Oudtshoorn Research Farm, South Africa. The resource population is described in Chapter 2.

The original dataset consisted of 3 656 records of slaughter ostriches from 119 (4 months) to 5 388 (>14 years) days of age, of which 3 137 were South African Black ostriches. Only data from birds slaughtered between 210 (7 months) and 540 (18 months) days of age were used for analyses, however, as this interval roughly typifies the plausible age range for slaughter bird production. Selection and treatment of slaughter birds was not standardized, resulting in large variation in slaughter age and weight across years and slaughter groups. This was partly due to experimental slaughtering over years for different purposes, as well as the slaughtering of breeder ostriches.

Ostriches were weighed on the farm, either before pre-slaughter isolation (approximately 14 days before slaughter) or before transportation to the abattoir, to obtain a pre-slaughter live weight. Slaughtering took place at a local European Union approved abattoir, according to standard techniques as described by Wotton & Sparrey (2002) and Hoffman (2012). The ostriches were fasted for 24 h, electrically stunned, hoisted by the legs and bled, before the feathers, skins, internal organs and abdominal fat were removed. After dressing, the drumsticks were cut from the carcasses, weighed and placed in a cooler for 24 h at approximately 2°C. The fan fillet (*Muscularis iliofibularis*) was dissected from the cooled right drumsticks of individual ostrich carcasses for further measurements.

A hand-held Crison pH/mV-506 pH meter equipped with a glass electrode was used to measure the ultimate pH (pH_{u}) and temperature of the *M. iliofibularis*, approximately 24 h after exsanguination.

Representative steaks (± 15 mm thick) were cut perpendicular to the muscle fibre direction (24 h *post-mortem*) in preparation for colour measurements and the determination of cooking and drip loss, respectively, according to the method described by Honikel (1998).

The colour of the fresh meat was evaluated after a blooming period of 30 minutes, by using a hand-held Gardner Color-guide colorimeter. Reflectance coordinates (L^* , a^* , b^*) of the Commission Internationale de l'Eclairage (1976) were measured in triplicate for each sample at randomly selected positions. The three repeated measurements of L^* , a^* and b^* values, indicating brightness or lightness, the red-green range (redness) and the blue-yellow range (yellowness), respectively, were averaged for statistical analysis.

For the drip loss determination, steaks were weighed and placed in netting and suspended in an inflated bag in such a manner that the exudates did not come into contact with the sample, but were collected in the bag (Honikel, 1998). After a storage period of 24 hours at 4°C, the samples were patted dry with absorbent paper and weighed again. Drip loss was expressed as a percentage of the initial weight of the sample. For cooking loss determination, the freshly cut (15 mm thick) steak was weighed, placed into sealed plastic bags and immersed in a water-bath at 75°C. After one hour the samples were removed from the water-bath and cooled under cold running water. The meat was removed from the packaging material, blotted dry and reweighed (Honikel, 1998). Cooking loss was computed as the weight loss of the sample after cooking expressed as a percentage of the initial sample weight.

Contemporary groups for live weight were as described in Chapter 2 and 3, representing year by season of hatch. Comparable live weight data from parents from the same contemporary groups as the slaughtered ostriches were also added to the analyses. The date of slaughter was used to define contemporary groups for slaughter and meat traits. Contemporary groups with less than 8 records were grouped with adjacent contemporary groups where possible, or removed from the data, resulting in 32 contemporary groups for live weight and 14 to 16 contemporary groups for the respective slaughter traits. The final dataset analysed consisted of 534 slaughter birds, the progeny of 180 sires and 177 dams, mated to each other in 202 unique combinations.

4.2.2 Statistical analysis

Measurements on instrumental meat quality were conducted irregularly, and approximately 500 records were available for each trait. A database of this size constitutes the bare minimum of records needed for the preliminary estimation of genetic parameters for these traits. Against this background, the data were analysed with a linear mixed animal model using ASReml (Gilmour *et al.*, 2009).

Fixed effects tested for all traits included age, contemporary group and gender (male or female). Two-way interactions between these effects were also included in the initial models. Fixed effects found to be significant were fitted in the final models for each trait.

Variance components were estimated by REML procedures fitting an animal model. In view of the size of the database it was not attempted to partition the animal effects in direct and maternal permanent environmental components. Given the nature of the data (instrumental quality was only measured on slaughtered animals) dams would also not have records of themselves in the database to aid in the partitioning of variances. The full linear mixed model (in matrix notation) was:

$$y = X\beta + Z_1a + e$$

where y was the vector of observations for the respective slaughter or meat traits; β and a were vectors of fixed effects and direct genetic effects, respectively. X was an incidence matrix relating records to the fixed effects (β) and Z_1 was the corresponding incidence matrix relating direct genetic effects to y , while e was the vector of residuals. It was assumed that:

$$\text{Var}(a) = A\sigma_a^2 \text{ and } \text{Var}(e) = I\sigma_e^2$$

where A was the numerator relationship matrix accounting for relationships among animals, I was an identity matrix; σ_a^2 and σ_e^2 are the additive direct and residual variances, respectively.

Single-trait analyses were used to derive heritability estimates for six meat quality traits, namely lightness (L^*), redness (a^*), yellowness (b^*), ultimate (24 h post mortem) pH (pHu), cooking loss percentage and drip loss percentage. Subsequently, a seven-trait animal model including all meat quality traits as well as animal live weight (as defined in Chapter 3) was fitted. This allowed the calculation of all relevant correlations among traits, together with their respective standard errors. Models used for each trait within the multi-trait analysis were those developed in single-trait analyses. As the data available for live weight were the same as has been used in Chapter 3, modelling in the seven-trait model was based on this information.

All analyses included the full pedigree file, consisting of 6 541 individuals, the progeny of 378 sires and 376 dams, mated to each other in 541 unique combinations, as described in Chapter 3.

4.3 Results

4.3.1 Descriptive statistics

Means and standard deviations for the respective meat quality traits are presented in Table 4.1. The average slaughter age was 373 (s.d. = 76) days. The measurement of instrumental meat quality was not

always applied consistently, resulting in the number of observations (N) varying somewhat among traits. Drip loss was very variable with a coefficient of variation of greater than 50%, while pH_u showed little variation with a coefficient of variation that was below 10%.

Table 4.1 Means (\pm s.d.), coefficients of variation (CV) and ranges for ostrich meat quality traits measured on the *M. iliofibularis*

Meat quality traits	N	Mean	CV (%)	Range
Lightness (L^*)	459	34.86 \pm 3.56	10	23.06 - 44.06
Redness (a^*)	459	12.98 \pm 2.36	18	7.18 - 19.82
Yellowness (b^*)	459	8.16 \pm 1.72	21	3.61 - 12.67
Ultimate pH (pH _u)	457	6.1 \pm 0.3	5	5.57 - 7.32
Cooking loss (%)	441	34.1 \pm 6.2	18	16.2 - 59.1
Drip loss (%)	431	2.3 \pm 1.2	52	0.4 - 7.0

4.3.2 Fixed effects

Significant fixed effects ($P < 0.05$) for each trait are presented in Table 4.2. Age only influenced some of the meat quality traits. Regressions (\pm s.e.) on age amounted to 0.006 \pm 0.002 per day for redness (a^*), 0.005 \pm 0.002 per day for yellowness (b^*), -0.001 \pm 0.000 for pH_u and 0.011 \pm 0.005% per day for cooking loss. The interaction of age and contemporary group was significant for L^* , suggesting that age effects on L^* were not consistent for all slaughter groups. Regressions on age by contemporary group ranged from -0.037 \pm 0.009 to 0.054 \pm 0.031 per day for L^* .

Table 4.2 Significant^a fixed effects influencing ostrich meat quality traits as measured on the *M. iliofibularis*. The coefficient of determination (R^2) indicates the amount of variation explained by these effects

Meat quality traits	Slaughter group		Gender	Age x	Age x G	R^2	
	Age	(SG)	(G)	SG	G x SG		
Lightness (L^*)	n.s.	***	***	*	n.s.	n.s.	0.60
Redness (a^*)	*	***	n.s.	n.s.	n.s.	n.s.	0.63
Yellowness (b^*)	*	***	n.s.	n.s.	n.s.	n.s.	0.28
Ultimate pH (pH _u)	*	***	n.s.	n.s.	n.s.	n.s.	0.56
Cooking loss	*	***	**	n.s.	n.s.	n.s.	0.75
Drip loss	n.s.	***	n.s.	n.s.	n.s.	*	0.20

^a Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s.: not significant

Slaughter group affected all traits investigated. Such contemporary group effects often reflect short-term changes in management or slaughter day conditions, however, and since such changes are neither predictable nor repeatable, it is not reported. Gender influenced cooking loss and L^* , while drip loss was only influenced by gender within specific contemporary groups. Cooking loss was 34.39 \pm 0.15% for males and 33.41 \pm 0.15% for females, while L^* was 36.25 \pm 0.11 for males and 35.36 \pm 0.11 for females.

4.3.3 (Co)variance components, ratios and correlations

The inclusion of the direct genetic component as a random effect in the operational model resulted in an improved log-likelihood for L^* and pH_u (Table 4.3).

Table 4.3 Log-likelihood (LogL) values for models^a fitting different random effects for ostrich meat quality traits for *M. iliofibularis* in single-trait animal model analysis. The best model is denoted in bold

Meat quality traits	FE	FE + h ²
Lightness (L^*)	-660.444	-655.831
Redness (a^*)	-412.361	-410.500
Yellowness (b^*)	-419.071	-419.016
Ultimate pH	401.138	409.826
Cooking loss	-726.296	-725.653
Drip loss	-269.641	-269.367

^a FE: fixed effects only; h²: animal genetic effect

Although not significant for all traits, the direct genetic component was fitted as default for all traits. These single-trait analyses resulted in heritability estimates (h^2) that ranged between 0.02 (b^*) and 0.30 (L^* and pH_u) (Table 4.4).

The majority of these heritability estimates were not significant as reflected by standard errors exceeding half of the corresponding estimate. L^* and pH_u were the only traits that exhibited significant genetic variation when assessed relative to the corresponding standard error.

Table 4.4 (Co)variance components and ratios^a (\pm s.e.) for ostrich instrumental meat quality traits for the *M. iliofibularis* estimated from single-trait analyses

Meat quality traits	h^2	σ_a^2	σ_e^2	σ_p^2
Lightness (L^*)	0.30 \pm 0.12	1.582	3.618	5.200
Redness (a^*)	0.10 \pm 0.07	0.204	1.859	2.063
Yellowness (b^*)	0.02 \pm 0.07	0.047	2.078	2.125
Ultimate pH	0.30 \pm 0.11	0.016	0.037	0.053
Cooking loss	0.08 \pm 0.08	0.768	8.971	9.739
Drip loss	0.03 \pm 0.06	0.041	1.136	1.178

^a h^2 : direct heritability; σ_a^2 : direct additive variance; σ_e^2 : residual variance; σ_p^2 : total phenotypic variance

Results from the seven-trait model are depicted in Table 4.5. The heritability estimates for cooking loss and drip loss were similar, as were the estimates for a^* and b^* . The heritability estimates for L^* and pH_u were in the same range.

Table 4.5 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations for ostrich live weight (LW) and ostrich meat quality traits for the *M. iliofibularis* as estimated in multi-trait analyses

Trait ^a	LW	<i>L</i> *	<i>a</i> *	<i>b</i> *	pH _u	CL	DL
<i>Additive genetic correlations (h² in bold on diagonal)</i>							
LW	0.41 ± 0.07	0.40 ± 0.19	0.35 ± 0.30	0.26 ± 0.36	-0.49 ± 0.17	0.04 ± 0.34	0.72 ± 0.30
<i>L</i> *		0.37 ± 0.12	-0.28 ± 0.34	0.56 ± 0.41	-0.65 ± 0.19	0.30 ± 0.38	0.46 ± 0.36
<i>a</i> *			0.13 ± 0.08	0.26 ± 0.49	-0.05 ± 0.34	0.24 ± 0.50	0.45 ± 0.50
<i>b</i> *				0.10 ± 0.10	-0.73 ± 0.43	0.61 ± 0.57	0.56 ± 0.61
pH _u					0.42 ± 0.12	-0.53 ± 0.31	-0.59 ± 0.34
CL						0.11 ± 0.09	0.42 ± 0.53
DL							0.11 ± 0.08
<i>Residual correlations (σ²_e in bold on diagonal)</i>							
LW	83	-0.19 ± 0.12	0.23 ± 0.08	0.05 ± 0.09	0.10 ± 0.12	0.00 ± 0.14	-0.07 ± 0.09
<i>L</i> *		3.36	-0.19 ± 0.09	0.06 ± 0.10	0.00 ± 0.14	0.21 ± 0.10	0.13 ± 0.10
<i>a</i> *			1.82	0.32 ± 0.07	-0.40 ± 0.09	0.12 ± 0.08	0.09 ± 0.07
<i>b</i> *				1.95	-0.11 ± 0.10	0.18 ± 0.08	0.14 ± 0.07
pH _u					0.032	-0.36 ± 0.09	-0.25 ± 0.09
CL						8.65	0.26 ± 0.07
DL							1.08
<i>Phenotypic correlations (σ²_p in bold on diagonal)</i>							
LW	141	0.04 ± 0.06	0.25 ± 0.05	0.09 ± 0.06	-0.15 ± 0.06	0.01 ± 0.06	0.11 ± 0.06
<i>L</i> *		5.32	-0.20 ± 0.05	0.16 ± 0.05	0.22 ± 0.05	0.19 ± 0.05	0.32 ± 0.04
<i>a</i> *			2.10	0.32 ± 0.04	-0.16 ± 0.05	0.14 ± 0.05	0.27 ± 0.10
<i>b</i> *				2.18	-0.23 ± 0.05	0.23 ± 0.05	0.19 ± 0.05
pH _u					0.056	-0.38 ± 0.05	-0.61 ± 0.12
CL						9.75	0.28 ± 0.05
DL							1.22

^a LW: live weight; *L**: lightness; *a**: redness; *b**: yellowness; pH_u: ultimate pH; CL: cooking loss; DL: drip loss

The genetic correlations of live weight with drip loss were high, while there was a negative genetic correlation between live weight and pH_u, suggesting that the meat from birds that had lower live weights would have a higher pH_u. Genetic correlations among meat quality traits were variable in sign and magnitude and generally not significant when assessed relative to the corresponding standard errors. The exception to this rule was a negative genetic correlation between *L** and pH_u that amounted to -0.65.

Residual and phenotypic correlations were variable, but mostly resembled the corresponding genetic correlations as far as direction was concerned. Phenotypic correlations among the meat quality traits were all significant.

4.4 Discussion

4.4.1 Descriptive statistics

The mean value for cooking loss found in this study was similar to the cooking loss of 36% reported by Sales (1996). Leygonie *et al.* (2012) accordingly reported drip loss and cooking loss of the *M. iliofibularis* to be 1.26% and 40.27%, respectively. These values are in the same range as the means obtained in this study.

The colour values of the *M. iliofibularis* were slightly different than those reported in previous studies, although still within range when also considering the corresponding standard deviations. Leygonie *et al.* (2012) reported respective values of 28.47 for L^* , 19.62 for a^* and 14.28 for b^* . The mean pH_u was in the same range as those reported earlier by Sales (1996) and Leygonie *et al.* (2012).

Drip loss was the only trait that was highly variable. The fixed effects fitted only explained 20% of the variation in this trait. It is therefore clear that drip loss was influenced by other factors that could not be accounted for. The rate of pH decline is one such factor that could influence drip loss. The low variation in pH_u is expected as, while immediate stress before slaughter and cooling after slaughter influence the rate of pH decline, by 24 hours *post mortem*, long term stress (if any) would be the only influence on pH. The ostriches were transported over a very short distance and were used to being handled. One can assume that the ostriches were thus not overly stressed and would expect a minimal effect on pH_u .

4.4.2 Fixed effects

In contrast to quantitative meat traits, which were mostly dependent on age (see Chapter 3), qualitative ostrich meat traits were not as dependent on age. The significant influence of age on cooking loss indicates that the water-holding capacity of the *M. iliofibularis* decreased with age, while pH_u also decreased with age. This is to be expected against the background of the relationship between water-holding capacity and pH.

Age did not influence L^* significantly, but seemed to influence a^* and b^* . Mellett (1995) indicated that meat derived from younger ostriches is lighter in colour than that derived from older birds. Hoffman & Fisher (2001) subsequently indicated that an increase in age was accompanied with a significant reduction in reflectance (L^*) and a significant increase in both a^* and b^* values, the meat thus becoming darker, redder and yellower with an increased age. The significant influences of age on a^* and b^* support the findings of Hoffman & Fisher (2001), as values for both traits increased significantly with age. The two colour measurements are known to be closely correlated to the amount of myoglobin and it is well known that as animals (and ostriches) age, the amount of myoglobin also increases (Hoffman & Fisher, 2001). Also, it could be that the age range reported here (210 – 540 days) was too narrow to show a significant age effect on L^* , whereas Hoffman & Fisher (2001) compared 14-month-old birds with 8-year-old breeder birds.

Nonetheless, age did interact with slaughter group for L^* , indicating that age possibly influenced L^* within some slaughter groups.

According to Hoffman *et al.* (2005), pH_u is one of the most important post-slaughter factors influencing the colour of meat, especially the L^* reading. It seems, however, that L^* , a^* and b^* values are influenced by different factors, and that these are slightly different from the factors influencing pH_u . On the other hand, it was clear that contemporary slaughter groups significantly influenced all traits and these effects could have masked some of the less pronounced effects, as could be deduced from the significant interactions of contemporary group with age and gender for some traits. Ostrich muscle colour and pH_u are susceptible to factors such as pre-slaughter transport (Hoffman *et al.*, 2012) and lairage stress (Van Schalkwyk *et al.*, 2005), which would differ between slaughter groups.

It is important to note that age will presumably also affect ostrich meat quality through the accumulation and maturation of collagen fibres, which leads to toughening of meat (Sainz & Cabbage, 1997; Hoffman & Fisher, 2001), although tenderness or tensile strength of ostrich meat was not reported here.

A gender effect was apparent on cooking loss and L^* , as well as on drip loss in specific slaughter groups. In contrast, Van Schalkwyk *et al.* (2005) found no gender influence on any of these meat quality traits. However, Hoffman *et al.* (2009) also recently reported differences attributable to gender in colorimetric values, cooking and drip loss recorded on ostrich fan fillet samples.

4.4.3 (Co)variance components, ratios and correlations

Heritability estimates from the multi-trait analysis were generally improved relative to single-trait estimates. L^* and pH_u showed significant genetic variation. Although no other heritability estimates for meat quality traits in ostriches are available for comparison, it is known that meat quality traits in other species also show significant genetic variation. Estimates of heritability for objective assessments of meat colour (reflectance, L^* , a^* and b^* values) and water-holding traits (drip loss and cooking loss percentage) for beef, which are comparable to ostrich meat in colour, are between 0.10 and 0.25 (Burrow *et al.*, 2001). The opportunity for genetic improvement in beef and the meat of Merino sheep was reported to be somewhat limited, though, due to low to moderate heritability estimates, associated with low levels of phenotypic variance for the meat quality traits (Greeff *et al.*, 2008; Warner *et al.*, 2010). However, high heritability estimates were reported for broiler chickens (Le Bihan-Duval *et al.*, 2001), indicating that improvement of meat quality in chickens is possible.

Estimates of genetic correlations had high standard errors, presumably because of the low number of records available for meat quality traits. The only significant genetic correlation was a negative genetic correlation between meat lightness (L^*) and pH_u . The direction of this correlation suggested that meat with a higher pH_u will also tend to be darker – a phenomena well known to occur in meat, leading to the dry, firm and dark syndrome. The lower the pH_u of meat, the closer the meat proteins are to their iso-electric point

and the weaker the water binding capacity (Estévez, 2011). A low water binding capacity implies more liquid on the cut surface and thus increased light reflectance. Meat with a high pH_u will have a strong water binding capacity which, amongst others, causes the muscle fibres to be swollen leading to light being absorbed by the surface and causing it to be perceived as being dark. Le Bihan-Duval (2004) also reported a strong negative correlation between these two traits for broiler chicken breast meat (-0.91 ± 0.02) and for turkey breast meat (-0.53 ± 0.19). In poultry meat, pH_u appeared to be a determining factor of meat quality, as significant negative correlations were obtained between this trait and the lightness as well as the drip loss of the raw product (Le Bihan-Duval, 2004). Similar results were apparent in this study, supporting this contention. The genetic correlation of pH_u with both drip loss and cooking loss was negative.

Redness and yellowness (a^* and b^*) had positive phenotypic relationships, which is consistent with expectation from similar studies in other species (Boukha *et al.*, 2011).

The characteristic high pH_u value for ostrich meat is conducive to the development of micro-organisms and a reduced shelf life and is therefore a determining factor for meat microbial quality and shelf life. Improvement of the shelf-life of ostrich meat is crucial, both for the local markets and for export.

Despite the high heritability estimate obtained, ultimate pH has a low phenotypic variance (as reflected by a coefficient of variation of 5%), however, which might limit genetic progress. Many non-genetic factors also influence post-mortem pH, among others pre-slaughter transport and lairage conditions (Van Schalkwyk *et al.*, 2005; Hoffman *et al.*, 2012), slaughter method, deboning, packaging and storage conditions (Hoffman *et al.*, 2008, 2009, 2012).

4.5 Conclusions

It must be conceded that the number of records available for studying instrumental ostrich meat quality was at the bare minimum for studies of this nature. Nonetheless, significant genetic variation in L^* and pH_u was demonstrated. Since pH_u has strong relationships with the colour and water-holding capacity of meat, which is important with regard to meat quality, it could be considered as an appropriate criterion for selection that should be further investigated. To optimise the efficiency of selection interactions with pre-slaughter stresses will have to be specified, however, as these can strongly affect pH_u .

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CHAPTER 5

Estimation of environmental and genetic factors influencing ostrich slaughter and skin traits

5.1 Introduction

Ostrich leather is considered one of the cornerstones of the South African ostrich industry. The skin of an ostrich is processed into unique leather that is in high demand due to its distinctive quill pattern, durability and suppleness. It competes in the exotic leather market, and is marketed as a luxury product due to its limited availability and unique appearance (Cooper, 2001).

Because of its use in the luxury products market, leather quality is of extreme importance to the local ostrich industry. The improvement of the quality of ostrich leather was accordingly identified as one of the key issues that need to be addressed for the South African ostrich industry to retain its competitive edge in the global market (National Agricultural Marketing Council, 2003). The knowledge base pertaining to ostrich leather quality is limited, however, despite the value and importance of leather to the industry (Sales, 1999; Engelbrecht *et al.*, 2009).

The size of the skin, the occurrence of visible defects and the appearance of the feather nodules collectively determine the quality and value of ostrich leather (Mellett, 1995; Engelbrecht *et al.*, 2005; 2009). Since the feather follicles are responsible for the unique appearance of ostrich leather, it is not surprising that the appearance of these follicles is of importance (Mellett, 1995; Engelbrecht *et al.*, 2009). However, only a part of the skin is covered with feather follicles and has this nodulated appearance. The biggest continuous nodulated area is the diamond-shaped area on the back of the ostrich, commonly referred to as the crown area. This is the most valuable part of the skin and the relative size of the crown is therefore important. The neckline (a narrow featherless strip that extends from the neck backwards into the crown) divides this continuous nodulated area is therefore also of importance, since it influences the cutting value of the leather. Cutting value can be defined as the size of the largest continuous nodulated panel that can be obtained from a specific skin. Skin thickness is also deemed to be important with regard to the size of the feather follicles (Mellett, 1995).

It has been demonstrated that certain skin quality factors, such as physical or visual damage to skins can be managed to some degree through improved slaughter practices or alternative management practices (Meyer, 2003). The influence of management practices on skin nodule traits and crown traits is largely unknown, however, but indications are that the potential to manipulate qualitative traits, such as nodule quality, through nutrition (Brand *et al.*, 2004; Cloete *et al.*, 2006) and other management regimes is limited.

Genetic selection may provide the industry with more scope for progress, since many traits are thought to be under genetic control. The success of genetic improvement as a tool for improved productivity has been well documented in other livestock industries. However, accurate genetic parameters are needed to determine whether there is sufficient scope for the genetic improvement of quantitative and qualitative skin traits.

A resource of available chrome-crusted ostrich skins was consequently evaluated for estimation of genetic and environmental parameters for various skin traits, to investigate the possibility of the genetic improvement of ostrich skin quality and likely correlated responses in slaughter traits following selection for skin quality.

5.2 Materials and methods

5.2.1 Data description

Pedigree and slaughter data were obtained from the commercial ostrich breeding flock maintained at the Oudtshoorn Research Farm, South Africa, as described in Chapter 2 and 3. The ostriches were raised predominantly in feedlot conditions with ostrich diets and potable drinking water being provided *ad libitum*. The flock consists mostly of the South African Black strain (*Struthio camelus domesticus*) and only data from this genotype were used for this study.

Progeny from the flock were periodically slaughtered as described in Chapter 3. Data from ostriches slaughtered between 1997 and 2008 were used for the estimation of genetic parameters for slaughter traits. Slaughter and skin data were matched with the on-farm records of each ostrich to link pedigree information to the data. The effects of year and rearing group were combined into the single effect of contemporary group, as described in Chapter 2.

Selection and treatment of slaughter groups was not standardized, resulting in large variation in slaughter age and weight across years and slaughter groups. The original dataset consisted of 3 736 records of slaughter ostriches from 119 to 5 388 days of age, of which 3 215 were South African Black ostriches. The large variation in age was mainly due to experimental slaughtering over years for different purposes, as well as slaughtering of breeder ostriches culled on account of age or non-production.

Only data from South African Blacks, slaughtered between 240 and 500 days of age were used for analyses, however, as this interval roughly typifies the plausible age range for slaughter bird production. The final dataset analysed consisted of 2 007 records, representing data from 1 703 slaughter ostriches and 304 breeder birds with comparable weight data, the progeny of 305 sires and 297 dams, mated to each other in 386 unique combinations.

Ostriches were weighed on the farm, either before pre-slaughter isolation (14 days before slaughter) or before transportation to the abattoir, to obtain a pre-slaughter live weight. The date of weighing was recorded in each instance and the age at weighing was consequently available. Comparable live weight data from birds selected as breeding material from the same contemporary groups as the slaughtered ostriches were also added to the analyses and subsequently defined as pre-slaughter live weight.

Only data from ostriches slaughtered at the local abattoir were used. Abattoir and tannery practices were not constant over years, however, with some measurements unfortunately only recorded for specific time periods. For instance, changes in the industry resulted in recording of raw skin data to be gradually replaced with crust skin determination only. Some skins consequently had either raw or crust skin data available, while some had both. For slaughter traits the slaughter group (defined as all ostriches slaughtered together on the same date) was used as contemporary group to account for changes in processing practices over time. Contemporary and slaughter groups consisting of less than seven individuals were deleted.

Slaughter data included *post mortem* weight (after stunning and bleeding out), skin traits (raw and crust skin size, raw and crust skin grading, crust skin weight and leather thickness), crown traits (crown dimensions i.e. crown width, length and shape) as well as neckline traits (neckline dimensions i.e. total neckline length, neckline length within the crown area, neckline width at the top of the crown and neckline width in the middle of the crown).

The size and grading (grade 1 - 5, with grade 5 representing the worst grade) of the raw skins was determined by the tannery shortly after slaughter. The skins were then processed and chrome-cruled according to standard tannery procedures (Meyer, 2003), after which the skins were measured and graded again. The size and grading information of the skins were obtained from the tannery.

The chrome-cruled skins were subsequently temporarily removed from the tannery to do various additional measurements on the chrome-cruled skins. These included weighing of the processed skin, measuring of the crown and neckline, and determination of leather thickness.

Leather thickness was measured with a calliper on the right hand side of the skin, next to and outside of the crown area. The approximate location of these measurements is shown in Figure 5.1. Three separate measurements were taken to obtain an average thickness for each skin.

The width of the crown area was determined by measuring the distance between the two farthest nodules on the horizontal median of the skin at the broadest point of the crown. The broadest point is situated between the two legs, slightly to the back of the ostrich (Figure 6.1). The crown length was measured from the narrowest point of the nodulated area at the neck to the end of the nodulated area at the rump.

Crown shape was defined as the shape or rounding of the crown area on the shoulder area of the skin, before indenting towards the elongated neck area. It was expressed as the distance (radius) between the

middle of the horizontal median (broadest part of the crown) and the furthest nodule on the crown's outer edge rounding, at an angle of approximately 30° (see Figure 6.1). Crown shape measurements were done on the right hand side of each skin. Crown area was estimated by calculating the area as an ellipse (πab), using π (crown width/2) x (crown length/2).

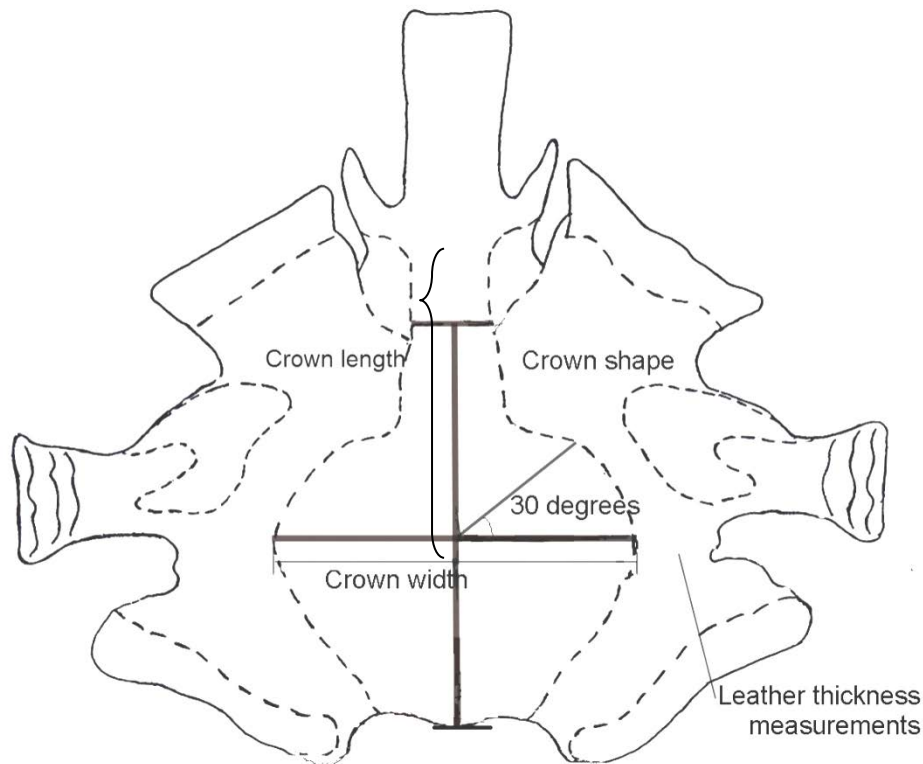


Figure 5.1 Measurements taken of the crown area and leather thickness

The total length of the neckline was also measured (NLTL), as well as the neckline length within the crown (NLLC), as indicated in Figure 5.2. The width of the neckline was measured at the top of the crown (NLWT) and in the middle of the crown (NLWM).

The neckline area within the crown was subsequently estimated by calculating the area as a trapezium, using the formula $1/2(NLWT + NLWM) \times NLLC$. The total neckline area was also estimated by calculating the area as an ellipse, using the formula $\pi (NLTL/2) \times (NLWT/2)$. These measurements were used to get an indication of the size of the neckline since tracing the area and determining the real area would have been time-consuming and unpractical due to a lack of easily available equipment.

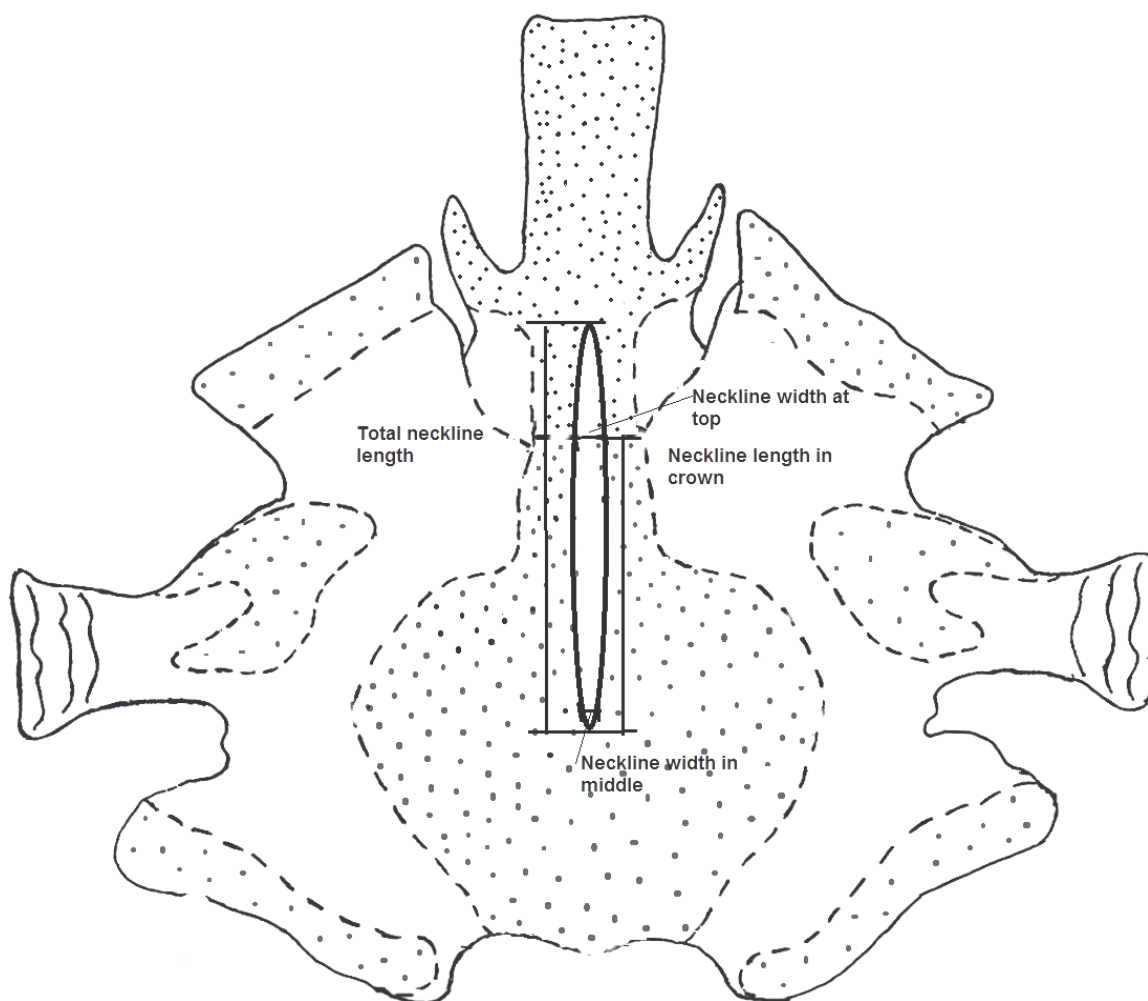


Figure 5.2 Measurements taken of the neckline on ostrich skins

5.2.2 Statistical analysis

The ASReml program (Gilmour *et al.*, 2009) was used to estimate fixed effects and subsequently to derive variance components and ratios for the respective slaughter and skin traits. Fixed effects considered included contemporary group and gender (male or female).

Age at measurement or slaughter was fitted as a linear covariate for all traits. The first analysis involved fitting various combinations of fixed effects and interactions between them to obtain an operational model for each trait. Effects found to be significant ($P < 0.05$) in preliminary analyses were retained in subsequent analyses.

The random genetic effects of animal and maternal permanent environment were added sequentially to the operational model. Maternal permanent environmental effects were also fitted per dam year because the

majority of dams had data of progeny hatched in more than one year recorded. The full linear mixed model (in matrix notation) fitted was as follows:

$$y = X\beta + Z_1a + Z_2m + Z_3pe + Z_3w + e$$

where y was a vector of observations for the respective weight traits and β , a , m , pe and w were vectors of fixed effects, direct and maternal additive genetic effects, maternal permanent environmental effects and within year permanent environmental effects, respectively. X was an incidence matrix relating records to the fixed effects (β), Z_1 , Z_2 and Z_3 were the corresponding incidence matrices relating the observations to the respective random effects, while e was the vector of residual effects. It was assumed that:

$$\text{Var}(a) = A\sigma_a^2; \text{Var}(m) = A\sigma_m^2; \text{Var}(pe) = I\sigma_{pe}^2; \text{Var}(w) = I\sigma_w^2 \text{ and } \text{Var}(e) = I\sigma_e^2,$$

where A was the numerator relationship matrix between animals, I was an identity matrix and σ_a^2 , σ_m^2 , σ_{pe}^2 , σ_w^2 and σ_e^2 were the additive direct, additive maternal, maternal permanent environmental, within year permanent environmental and residual variances, respectively.

Log-likelihood tests were conducted to determine the most suitable random effects model for each trait in single-trait analyses by sequentially testing the addition of one parameter at a time (Snyman *et al.*, 1996). This was followed by two-trait models to determine the correlations between live weight, which is easily measurable on all live animals, and slaughter traits. The reasoning behind this step was to determine to what extent pre-slaughter live weight could be used as a proxy for those traits recorded after slaughter.

Subsequently, several multi-trait animal models were fitted for calculation of all relevant correlations among traits. Models used for each trait within the multi-trait analysis were those developed in single-trait analyses.

The multi-trait models included models relating pre-slaughter live weight with skin traits, crown traits and neckline traits, respectively. Live weight was subsequently added as a covariate for analyses of the above-mentioned traits. These analyses were done to establish whether genetic variation would remain after the quantitative measurements were scaled for size. The latter analyses were subsequently repeated for models where it was deemed important, based on the results obtained, replacing pre-slaughter live weight with *post mortem* weight and crust skin size, respectively, to compare the effect of using these traits as covariates to account for size. This was done with a reduced dataset containing no missing values for the respective covariates.

All analyses included the full pedigree file, consisting of 6 503 individuals, the progeny of 375 sires and 375 dams, mated to each other in 537 unique combinations. Individuals hatched from generation one through seven were included. The pedigree was built by using all available ancestors with appropriate live weight and skin data, hence the slight difference from the pedigree file used for the analysis of meat traits.

5.3 Results

5.3.1 Descriptive statistics

The mean (\pm s.d.) age of the ostriches slaughtered were 383 (\pm 57) days, ranging from 242 to 498 days old. There were 33 contemporary groups and 44 slaughter groups for analyses. The average size of contemporary and slaughter groups was 61 and 39, respectively.

Descriptive statistics (means, standard deviations, coefficients of variation and range) for the respective slaughter and skin traits are presented in Table 5.1.

Table 5.1 Means (\pm s.d.), coefficients of variation (CV) and ranges for ostrich slaughter and skin traits

Trait	N	Mean \pm s.d.	CV (%)	Range
<u>Slaughter traits:</u>				
Live weight (kg)	2 007	92.7 \pm 17.2	19	26 – 148
Post mortem weight (kg)	1 232	83.2 \pm 14.6	18	34.3 - 134.7
<u>Skin traits:</u>				
Raw skin size (dm ²)	1 267	131 \pm 12	9	78 – 158
Crust skin size (dm ²)	1 104	140 \pm 12	9	78 – 178
Raw skin grade	1 279	1.6 \pm 0.7	44	1 – 4
Crust skin grade	1 104	2.2 \pm 1.1	50	1 – 5
Crust skin weight (kg)	1 237	0.823 \pm 0.191	23	0.255 - 1.721
Leather thickness (mm)	1 295	0.80 \pm 0.30	38	0.30 - 2.00
<u>Crown traits:</u>				
Crown width (mm)	1 291	658 \pm 43	7	505 – 839
Crown length (mm)	1 270	822 \pm 65	8	474 – 1030
Crown shape (mm)	1 292	283 \pm 29	10	187 – 414
Crown area (dm ²)	1 267	42.6 \pm 5.1	12	22.7 - 59.2
<u>Neckline traits:</u>				
Total neckline length (mm)	1 259	623 \pm 56	9	374 – 863
Neckline length in crown (mm)	1 261	481 \pm 48	10	214 – 640
Neckline width at top (mm)	1 288	35 \pm 7	20	4 – 62
Neckline width in middle (mm)	1 274	18 \pm 4	22	7 – 35
Neckline area in crown (dm ²)	1 252	1.28 \pm 0.27	21	0.38 - 2.28
Total neckline area (dm ²)	1 258	1.73 \pm 0.40	23	0.45 - 3.28

N: number of records; CV: coefficient of variation

Skin size and crown traits had coefficients of variation below 12%, while most other traits were more variable. Skin grading and leather thickness had the highest coefficients of variation.

5.3.2 Fixed effects

Significant fixed effects for each trait are presented in Table 5.2.

Table 5.2 Significant^a fixed effects influencing slaughter and skin traits

Trait	Age ^b	Contemporary group (CG) ^c	Gender (G)	Age x CG	Age x G	G x CG	R ²
<u>Slaughter traits:</u>							
Live weight	***	***	n.s.	***	n.s.	n.s.	0.51
Post mortem weight	***	***	n.s.	***	n.s.	n.s.	0.50
<u>Skin traits:</u>							
Raw skin size	***	***	n.s.	***	n.s.	n.s.	0.45
Crust skin size	***	***	n.s.	**	n.s.	n.s.	0.47
Raw skin grade	n.s.	***	n.s.	*	n.s.	n.s.	0.12
Crust skin grade	n.s.	***	n.s.	n.s.	n.s.	n.s.	0.40
Crust skin weight	***	***	***	**	***	n.s.	0.50
Leather thickness	***	***	***	n.s.	**	n.s.	0.64
<u>Crown traits:</u>							
Crown width	*	***	n.s.	*	n.s.	n.s.	0.33
Crown length	**	***	**	n.s.	*	n.s.	0.47
Crown shape	**	***	n.s.	n.s.	n.s.	n.s.	0.33
Crown area	***	***	n.s.	n.s.	s	n.s.	0.42
<u>Neckline traits:</u>							
Total neckline length	n.s.	***	n.s.	n.s.	n.s.	n.s.	0.11
Neckline length in crown	n.s.	***	n.s.	n.s.	n.s.	n.s.	0.11
Neckline width at top	n.s.	***	*	n.s.	n.s.	n.s.	0.15
Neckline width in middle	n.s.	***	n.s.	n.s.	n.s.	n.s.	0.08
Neckline area in crown	n.s.	***	n.s.	n.s.	n.s.	n.s.	0.12
Total neckline area	n.s.	***	**	n.s.	n.s.	*	0.14

^a Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s.: not significant

^b For live weight, age refers to age at last live weighing while for the rest of the traits, age refers to age at slaughter

^c Contemporary group refers to slaughter group for all traits measured at or after slaughter

All the traits under consideration were dependent on age, with the exception of skin grading and neckline traits. Regressions (\pm s.e.) on age amounted to 0.193 ± 0.075 kg/day for live weight, 0.090 ± 0.10 dm²/day for crust skin size, -0.0024 ± 0.0019 kg/day for crust skin weight, 0.0011 ± 0.0003 mm/day for leather thickness and 0.020 ± 0.0054 dm²/day for crown size.

Contemporary group (or slaughter group) (CG) affected all traits investigated. Contemporary group effects often reflect short-term changes in climate and/or management, however, and since such changes are neither predictable nor repeatable, it is not reported. Ambient conditions and abattoir procedures at specific slaughter dates could similarly be involved in differences between slaughter groups.

In contrast to the insignificant effect of gender on live weight, gender influenced crust skin weight, leather thickness, crown length, neckline width at the top of the crown and the total size of the neckline. Males generally had thicker skins than females (0.87 ± 0.01 vs. 0.82 ± 0.01 mm respectively) and heavier crust skins than females (0.914 ± 0.004 vs. 0.832 ± 0.004 kg) when live weight was not accounted for. The crown length of skins from males were slightly longer (831 ± 2 vs. 823 ± 2 mm), while the necklines were slightly wider at the top of the crown (35.6 ± 0.2 vs. 34.9 ± 0.2 mm) and bigger (1.78 ± 0.02 vs. 1.74 ± 0.02 dm²) overall.

The significant Age x CG interaction for some of the traits suggests that age effects were not consistent for all contemporary groups. Regressions for live weight on age ranged from -0.818 ± 0.193 to 0.587 ± 0.370 between contemporary groups. Similarly, the age effect for crust skin weight, leather thickness and crown length were different for males and females, as suggested by the significant Age x G interaction.

5.3.3 (Co)variance components, ratios and correlations

5.3.3.1 Single-trait results

Log-likelihood values under alternative models for random effects are presented in Table 5.3. The inclusion of the animal genetic component (h^2) as a random effect in the operational model resulted in an improved log-likelihood for all traits, with the exception of raw and crust skin grades.

Heritability estimates for raw skin grade (0.06) and crust skin grade (0.00) were accordingly not significant (Table 5.4). Due to the lack of genetic variation in skin grading, it was excluded from further analyses. The heritability estimate of crown length (0.11) was also not significant with a standard error of 0.07.

The heritability estimate for raw skin size was higher than the estimate for crust skin size. More records were also available for raw skin size versus crust skin size. However, further analysis was complicated by the fact that crust skin size completely replaced the measurement of raw skin size from 2006 onwards. As the genetic correlation between raw and crust skin size was calculated to be very high (0.97 ± 0.02), it was decided to only use crust skin size in subsequent analyses. However, crust skin size records were not available for all records in the period before 2006 when raw skin size was mostly measured. Raw skin size was consequently used to predict crust skin size for these records, using the equation ($1.088 \times \text{raw skin size} - 5.156$) ($r = 0.84$), which was derived from skins where both traits were recorded. It is conceded that the correlation is on the low side for a prediction equation, where a higher level of accuracy would be a bonus. The correlation is probably affected by the fact that crust skins are subjected to additional interventions such

as flaying as well as the trimming of the edges. These practices could certainly impact on the derived relationship. As the impact of these interventions would be expected to be random, it is unlikely that it would introduce a bias as far as specific families would be concerned. Bearing this in mind, it is reassuring that the correlation was still well above 0.8. It was furthermore evident that a linear regression fitted the data best, and that no other relationship provided a better fit.

Table 5.3 Log-likelihood (LogL) values for models^a fitting different random effects for ostrich slaughter and skin traits in single-trait animal model analysis. The best model is denoted in bold

Trait	FE	FE + h ²	FE + h ² + pe ²	FE + h ² + pe ² .yr	FE + h ² + pe ² + pe ² .yr
<u>Slaughter traits:</u>					
Live weight	-6023.47	-5949.74	-5943.25	-5945.77	-5941.99
Post mortem weight	-4791.83	-4719.51	-4714.48	-4718.05	-4714.10
<u>Skin traits:</u>					
Raw skin size	-3414.37	-3361.01	-3360.41	-3360.32	-3360.00
Crust skin size	-4710.64	-4652.70	-4650.18	-4650.96	-4649.34
Raw skin grade	-277.704	-276.612	-276.055	-276.229	-275.897
Crust skin grade	-421.978	-421.978	-421.776	-421.969	-421.776
Crust skin weight	1527.86	1551.88	1552.80	1552.44	1552.95
Leather thickness	1446.07	1459.59	1460.27	1461.67	1461.76
<u>Crown traits:</u>					
Crown width	-5144.02	-5088.23	-5083.18	-5086.94	-5082.92
Crown length	-5426.73	-5403.85	-5400.69	-5403.85	-5400.69
Crown shape	-4654.09	-4636.29	-4634.94	-4636.29	-4634.94
Crown area	-2348.78	-2303.07	-2298.23	-2302.68	-2298.23
<u>Neckline traits:</u>					
Total neckline length	-5509.08	-5472.14	-5472.03	-5472.14	-5472.03
Neckline length in crown	-5330.12	-5308.37	-5307.41	-5308.37	-5307.41
Neckline width at top	-3015.28	-2969.80	-2969.47	-2968.99	-2968.91
Neckline width in middle	-2436.43	-2421.40	-2421.40	-2420.98	-2420.98
Neckline area in crown	996.625	1037.13	1037.21	1037.19	1037.23

^a FE: fixed effects only; h²: animal genetic effect; pe²: maternal permanent environmental effect; pe².yr: maternal permanent environmental effect within year

The unique dam within year (pe².yr) effect resulted in an improved log-likelihood for leather thickness when added to the model as a single random effect additional to h². The addition of the maternal permanent environmental (pe²) effect resulted in an improved log-likelihood for live weight, crust skin size and all the crown traits, with the exception of crown shape.

The estimated pe² effects were only significant for live weight, crown width and crown area, however (Table 5.4). It bordered on significance (P = 0.05) for crust skin size and crown length. The pe².yr variance

estimated for leather thickness was also not significant according to the derived standard error. Heritability estimates obtained when excluding these effects, were 0.33 ± 0.06 for crust skin size, 0.22 ± 0.06 for leather thickness and 0.27 ± 0.07 for crown length.

Table 5.4 (Co)variance components and ratios^a (\pm s.e.) for ostrich slaughter and skin traits estimated from single-trait analyses

Trait ^b	h^2	pe^2	$pe^2.yr$	σ_a^2	σ_{pe^2}	$\sigma_{pe.yr^2}$	σ_e^2	σ_p^2
<u>Slaughter traits:</u>								
LW	0.20 ± 0.06	0.08 ± 0.03	-	29.7	11.7	-	105.0	146.3
PMW	0.22 ± 0.08	0.10 ± 0.03	-	21.6	9.9	-	69.0	100.5
<u>Skin traits:</u>								
RSZ	0.37 ± 0.07	-	-	30.1	-	-	50.3	80.5
CSS	0.20 ± 0.07	0.06 ± 0.03	-	18.1	5.18	-	66.7	89.9
RSG	0.06 ± 0.04	-	-	0.024	-	-	0.407	0.431
CSG	0.00 ± 0.00	-	-	0.000	-	-	0.731	0.731
CSW	0.24 ± 0.06	-	-	0.004	-	-	0.013	0.018
LT	0.18 ± 0.06	-	0.07 ± 0.04	0.006	-	0.002	0.025	0.033
<u>Crown traits:</u>								
CW	0.21 ± 0.09	0.12 ± 0.04	-	254	147	-	831	1232
CL	0.11 ± 0.07	0.08 ± 0.04	-	239	190	-	1823	2253
CS	0.20 ± 0.06	-	-	111	-	-	454	565
CA	0.18 ± 0.08	0.11 ± 0.04	-	2.81	1.66	-	10.7	15.2
<u>Neckline traits:</u>								
NLTL	0.28 ± 0.06	-	-	781	-	-	2017	2798
NLCL	0.23 ± 0.06	-	-	476	-	-	1601	2077
NLWT	0.31 ± 0.07	-	-	12.7	-	-	28.9	41.6
NLWM	0.18 ± 0.06	-	-	3.1	-	-	14.2	17.4
NLA	0.31 ± 0.07	-	-	0.020	-	-	0.044	0.064

^a h^2 : direct heritability; pe^2 : maternal permanent environmental effect; $pe^2.yr$: maternal permanent environmental effect within year; σ_a^2 : direct additive variance; σ_{pe^2} : maternal permanent environmental variance; $\sigma_{pe.yr^2}$: maternal permanent environmental variance within year; σ_e^2 : residual variance; σ_p^2 : total phenotypic variance

^b LW: pre-slaughter live weight; PMW: *post mortem* weight; RSZ: raw skin size; CSS: crust skin size; RSG: raw skin grade; CSG: crust skin grade; CSW: crust skin weight; LT: leather thickness; CW: crown width; CL: crown length; CS: crown shape; CA: crown area; NLTL: Neckline total length; NLCL: Neckline length in crown; NLWT: Neckline width at top of crown; NLWM: Neckline width in middle of crown; NLA: Neckline area in crown

5.3.3.2 Correlations obtained from two-trait analysis

The correlations among pre-slaughter live weight and skin traits as estimated in two-trait models are presented in Table 5.5. Genetic correlations between live weight and the other traits were all positive.

The genetic correlation between live weight and post mortem weight was unity, even though these weights were recorded at different times that were not equally spaced. Live weight could therefore be used in subsequent analyses, instead of post mortem weight, for which less records were available. This would ensure the inclusion of parent data in the analyses, since parents only had live weight records in the data.

The genetic correlations between live weight and leather thickness, neckline width at the top and neckline width in the middle of the crown area were not significantly different from zero. The genetic correlation of live weight with crust skin weight and all the crown traits was higher, while genetic correlations of live weight with neckline traits were generally low or not significant. Environmental and phenotypic correlations between live weight and these traits were correspondingly low. The maternal permanent environmental correlations, where applicable, were high and ranged between 0.69 (crown width) and 0.99 (crust skin size) between live weight and the respective skin traits.

Table 5.5 Estimates of genetic (r_g), maternal permanent environmental (r_c), environmental (r_e) and phenotypic (r_p) correlations (\pm s.e.) among ostrich pre-slaughter live weight and skin traits from two-trait models

Trait	Correlated trait	r_g	r_c	r_e	r_p
Live weight X	<i>Post mortem</i> weight	1.00 \pm 0.01	1.00 \pm 0.02	0.83 \pm 0.02	0.89 \pm 0.01
	<u>Skin traits</u>				
	Crust skin size	0.84 \pm 0.09	0.99 \pm 0.08	0.71 \pm 0.02	0.75 \pm 0.01
	Crust skin weight	0.66 \pm 0.11		0.68 \pm 0.03	0.66 \pm 0.02
	Leather thickness	0.25 \pm 0.23		0.19 \pm 0.05	0.18 \pm 0.03
	<u>Crown traits</u>				
	Crown width	0.64 \pm 0.19	0.69 \pm 0.17	0.56 \pm 0.04	0.59 \pm 0.02
	Crown length	0.98 \pm 0.13	0.81 \pm 0.14	0.44 \pm 0.03	0.54 \pm 0.02
	Crown shape	0.80 \pm 0.13		0.27 \pm 0.04	0.37 \pm 0.03
	Crown area	0.91 \pm 0.12	0.80 \pm 0.11	0.60 \pm 0.03	0.67 \pm 0.02
	<u>Neckline traits</u>				
	Total neckline length	0.57 \pm 0.15		0.24 \pm 0.05	0.31 \pm 0.03
	Neckline length in crown	0.42 \pm 0.18		0.22 \pm 0.05	0.26 \pm 0.03
	Neckline width at top	0.35 \pm 0.19		0.20 \pm 0.05	0.22 \pm 0.03
	Neckline width in middle	0.27 \pm 0.23		0.09 \pm 0.05	0.12 \pm 0.03
	Neckline area in crown	0.49 \pm 0.18		0.27 \pm 0.05	0.30 \pm 0.03

5.3.3.3 Multi-trait results

Results from a multi-trait model that included live weight and skin traits (crust skin size, crust skin weight and leather thickness) are given in Table 5.6. The estimate for the maternal permanent environmental effect by year for leather thickness was excluded from the analysis, following the single-trait results where the estimate was not significant. Estimates of heritability (h^2) were similar to those from single-trait analyses. However, it seems that some of the variance for pe^2 repartitioned to h^2 in the multi-trait analysis for live weight and crust skin size.

Live weight and crust skin size were genetically very similar, with the genetic correlation not differing from unity (95% confidence intervals of 0.77 to 1.01). Genetic correlations of live weight and crust skin size with crust skin weight were positive and relatively high. The only significant genetic correlation involving leather thickness was with crust skin weight. The maternal permanent environmental correlation between live weight and crust skin size was very high at 0.94. Residual and phenotypic correlations were mostly comparable to genetic correlations in sign and magnitude.

Table 5.6 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations between ostrich slaughter and skin traits from a four-trait analysis

Trait	Live weight	Crust skin size	Crust skin weight	Leather thickness
<i>Additive genetic correlations (h^2 in bold)</i>				
Live weight	0.24 \pm 0.06	0.89 \pm 0.06	0.65 \pm 0.11	0.13 \pm 0.19
Crust skin size		0.23 \pm 0.06	0.66 \pm 0.11	0.06 \pm 0.19
Crust skin weight			0.23 \pm 0.05	0.41 \pm 0.17
Leather thickness				0.22 \pm 0.06
<i>Maternal permanent environmental correlations (pe^2 in bold)</i>				
Live weight	0.05 \pm 0.02	0.94 \pm 0.13	n.a.	n.a.
Crust skin size		0.03 \pm 0.01	n.a.	n.a.
<i>Residual correlations (σ_e^2 in bold)</i>				
Live weight	111	0.70 \pm 0.02	0.70 \pm 0.03	0.21 \pm 0.05
Crust skin size		71.5	0.71 \pm 0.03	0.18 \pm 0.05
Crust skin weight			0.015	0.44 \pm 0.04
Leather thickness				0.026
<i>Phenotypic correlations (σ_p^2 in bold)</i>				
Live weight	156	0.75 \pm 0.01	0.67 \pm 0.02	0.19 \pm 0.03
Crust skin size		92.4	0.69 \pm 0.02	0.15 \pm 0.03
Crust skin weight			0.019	0.43 \pm 0.03
Leather thickness				0.033

n.a.: parameter not applicable

The results of a multi-trait model including live weight as linear covariate are reported in Table 5.7.

Table 5.7 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations between ostrich skin traits from a three-trait analysis with live weight as linear covariate

Trait	Crust skin size	Crust skin weight	Leather thickness
<i>Additive genetic correlations (h^2 in bold)</i>			
Crust skin size	0.19 \pm 0.07	0.36 \pm 0.19	-0.17 \pm 0.24
Crust skin weight		0.33 \pm 0.07	0.44 \pm 0.16
Leather thickness			0.24 \pm 0.06
<i>Residual correlations (σ_e^2 in bold)</i>			
Crust skin size	43.1	0.46 \pm 0.05	0.05 \pm 0.05
Crust skin weight		0.007	0.41 \pm 0.05
Leather thickness			0.024
<i>Phenotypic correlations (σ_p^2 in bold)</i>			
Crust skin size	59.3	0.41 \pm 0.03	0.00 \pm 0.03
Crust skin weight		0.011	0.41 \pm 0.03
Leather thickness			0.032

The heritability estimate for crust skin weight was slightly improved, while the heritability estimate for crust skin size was lower. The maternal permanent environmental effect for crust skin size (not indicated in Table 5.7) amounted to 0.08 ± 0.03 in this analysis. The heritability estimate for leather thickness remained in the same range.

The genetic correlations of crust skin size with the other skin traits become insignificant, while the residual and phenotypic correlations between the skin traits were also significantly lower after live weight was included as a covariate. The only exception was the phenotypic correlation between crust skin weight and leather thickness, which remained largely unchanged.

Correlations from a multi-trait analysis that included crust skin size and the quantitative crown traits (crown width, crown length, crown shape and crown area) are presented in Table 5.8. The heritability of crown length remained insignificant, as in the single-trait analysis. The other heritability estimates were moderate, and similar to those obtained in single-trait analysis. Genetic correlations were very high between all the traits.

Maternal permanent environmental correlations were accordingly high where applicable, with the exception of the correlation between crown width and crown length.

Residual and phenotypic correlations were all positive and significant, and somewhat lower than the corresponding genetic correlations. The residual and phenotypic correlations involving crown shape were generally significantly lower than the corresponding correlations among the other traits.

Table 5.8 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations among ostrich skin crown traits from a five-trait analysis

Trait	Crust skin size	Crown width	Crown length	Crown shape	Crown area
<i>Additive genetic correlations (h^2 in bold)</i>					
Crust skin size	0.22 \pm 0.06	0.79 \pm 0.13	0.97 \pm 0.13	0.87 \pm 0.12	0.93 \pm 0.07
Crown width		0.19 \pm 0.08	0.75 \pm 0.27	0.88 \pm 0.17	0.95 \pm 0.07
Crown length			0.12 \pm 0.07	0.79 \pm 0.24	0.92 \pm 0.08
Crown shape				0.17 \pm 0.05	0.89 \pm 0.16
Crown area					0.19 \pm 0.07
<i>Maternal permanent environmental correlations (pe^2 in bold)</i>					
Crust skin size	0.05 \pm 0.02	0.75 \pm 0.16	0.79 \pm 0.17	n.a.	0.89 \pm 0.10
Crown width		0.11 \pm 0.03	0.45 \pm 0.25	n.a.	0.88 \pm 0.07
Crown length			0.06 \pm 0.03	n.a.	0.83 \pm 0.10
Crown area					0.09 \pm 0.03
<i>Residual correlations (σ_e^2 in bold)</i>					
Crust skin size	67	0.60 \pm 0.03	0.53 \pm 0.03	0.35 \pm 0.04	0.69 \pm 0.02
Crown width		873	0.31 \pm 0.04	0.23 \pm 0.04	0.77 \pm 0.02
Crown length			1853	0.07 \pm 0.04	0.84 \pm 0.01
Crown shape				466	0.17 \pm 0.05
Crown area					10.8
<i>Phenotypic correlations (σ_p^2 in bold)</i>					
Crust skin size	92	0.65 \pm 0.02	0.61 \pm 0.02	0.44 \pm 0.02	0.75 \pm 0.01
Crown width		1249	0.38 \pm 0.03	0.33 \pm 0.03	0.81 \pm 0.01
Crown length			2258	0.17 \pm 0.03	0.85 \pm 0.01
Crown shape				561	0.29 \pm 0.03
Crown area					15.0

n.a.: parameter not applicable

When live weight was included as a covariate for crust skin size and crown traits, heritability estimates and genetic correlations were substantially reduced (Table 5.9). The standard errors associated with these genetic correlations were also increased, rendering many of them within two standard errors from the estimate. The genetic correlation between crust skin size and crown area remained high and significant though. Residual and phenotypic correlations remained positive in most cases, the exceptions being those between crown length and crown shape.

Table 5.9 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations between ostrich skin crown traits from a five-trait analysis, including live weight as a linear covariate

Trait	Crust skin size	Crown width	Crown length	Crown shape	Crown area
<i>Additive genetic correlations (h^2 in bold)</i>					
Crust skin size	0.11 \pm 0.05	0.61 \pm 0.27	0.56 \pm 0.47	0.39 \pm 0.27	0.75 \pm 0.25
Crown width		0.13 \pm 0.08	0.16 \pm 0.63	0.56 \pm 0.31	0.87 \pm 0.18
Crown length			0.04 \pm 0.06	0.43 \pm 0.49	0.62 \pm 0.41
Crown shape				0.12 \pm 0.05	0.64 \pm 0.38
Crown area					0.08 \pm 0.07
<i>Maternal permanent environmental correlations (pe^2 in bold)</i>					
Crust skin size	0.01 \pm 0.02	0.43 \pm 0.49	0.65 \pm 0.77	n.a.	0.63 \pm 0.47
Crown width		0.10 \pm 0.04	0.11 \pm 0.49	n.a.	0.88 \pm 0.12
Crown length			0.02 \pm 0.03	n.a.	0.56 \pm 0.34
Crown area					0.06 \pm 0.03
<i>Residual correlations (σ_e^2 in bold)</i>					
Crust skin size	36	0.37 \pm 0.04	0.37 \pm 0.03	0.26 \pm 0.04	0.48 \pm 0.03
Crown width		626	0.11 \pm 0.04	0.11 \pm 0.04	0.67 \pm 0.02
Crown length			1517	-0.06 \pm 0.04	0.81 \pm 0.02
Crown shape				431	0.02 \pm 0.04
Crown area					7.12
<i>Phenotypic correlations (σ_p^2 in bold)</i>					
Crust skin size	42	0.39 \pm 0.02	0.38 \pm 0.02	0.27 \pm 0.03	0.50 \pm 0.02
Crown width		819	0.11 \pm 0.03	0.16 \pm 0.03	0.70 \pm 0.02
Crown length			1619	-0.03 \pm 0.03	0.78 \pm 0.01
Crown shape				487	0.08 \pm 0.03
Crown area					8.30

n.a.: parameter not applicable

Results from multi-trait models that included either *post mortem* weight or crust skin size as linear covariates are presented in Tables 5.10 and 5.11 for comparison. Heritability estimates obtained when using post mortem weight as covariate were similar to those obtained when live weight was used as a covariate, with only the h^2 estimate of crown shape being slightly lower. When including crust skin size as a linear covariate heritability estimates were somewhat lower than when weight was included as a covariate. In contrast to estimates of h^2 , variance ratios involving pe^2 were quite similar among analyses involving different traits as covariates.

Table 5.10 Genetic variance ratios for ostrich crown traits as estimated in various multi-trait analyses, with or without size as a linear covariate

Trait ^a	Linear covariate fitted			
	none	LW	PMW	CSS
<i>Estimates of heritability</i>				
CW	0.19 ± 0.08	0.13 ± 0.08	0.13 ± 0.10	0.04 ± 0.07
CL	0.12 ± 0.07	0.04 ± 0.06	0.04 ± 0.06	0.03 ± 0.07
CS	0.17 ± 0.05	0.12 ± 0.05	0.06 ± 0.04	0.08 ± 0.05
CA	0.19 ± 0.07	0.08 ± 0.07	0.09 ± 0.08	0.05 ± 0.07
<i>Estimates of maternal permanent environment variance</i>				
CW	0.11 ± 0.03	0.10 ± 0.04	0.11 ± 0.05	0.13 ± 0.04
CL	0.06 ± 0.03	0.02 ± 0.03	0.04 ± 0.04	0.05 ± 0.04
CA	0.09 ± 0.03	0.06 ± 0.03	0.09 ± 0.04	0.08 ± 0.04

^a LW: pre-slaughter live weight; PMW: *post mortem* weight; CSS: crust skin size; CW: crown width; CL: crown length; CS: crown shape; CA: crown area

Genetic correlations (Table 5.11) were not significant when adding crust skin size as a covariate. Correlations among crown width and crown length with crown area remained high when including live weight as a covariate.

Table 5.11 Genetic and phenotypic correlations for ostrich crown traits as estimated in various multi-trait analyses, with or without size as a linear covariate

Trait ^a	Correlated trait	Without LW / CSS		With LW		With CSS	
		r _g	r _p	r _g	r _p	r _g	r _p
CW	CL	0.75 ± 0.27	0.38 ± 0.03	0.16 ± 0.63	0.11 ± 0.03	0.30 ± 1.39	-0.01 ± 0.03
	CS	0.88 ± 0.17	0.33 ± 0.03	0.56 ± 0.31	0.16 ± 0.03	0.75 ± 0.76	0.03 ± 0.03
	CA	0.95 ± 0.07	0.81 ± 0.01	0.87 ± 0.18	0.70 ± 0.02	0.81 ± 0.56	0.64 ± 0.02
CL	CS	0.79 ± 0.24	0.17 ± 0.03	0.43 ± 0.49	-0.03 ± 0.03	-0.10 ± 0.74	0.15 ± 0.03
	CA	0.92 ± 0.08	0.85 ± 0.01	0.62 ± 0.41	0.78 ± 0.01	0.80 ± 0.49	0.76 ± 0.01
CS	CA	0.89 ± 0.16	0.29 ± 0.03	0.64 ± 0.38	0.08 ± 0.03	0.37 ± 0.66	-0.10 ± 0.03

^a LW: pre-slaughter live weight; CSS: crust skin size; CW: crown width; CL: crown length; CS: crown shape; CA: crown area

Results from a multi-trait model including crust skin size and neckline traits (neckline total length, neckline length in crown; neckline width at top of crown, neckline width in the middle of the crown and neckline area within the crown) are given in Table 5.12.

Estimates of h² were moderate for all the neckline traits, while genetic correlations varied from low and insignificant (between neckline length in crown and neckline width at top of crown) to high and significant (between total neckline length and neckline length in crown). The other neckline traits were all related to the neckline size, the genetic correlations ranging from moderate for neckline length in crown to very high for neckline width at the top. The residual and phenotypic correlations among neckline traits were all positive

and mostly within the same range as the corresponding genetic correlations. The estimate of pe^2 for crust skin size amounted to 0.06 ± 0.03 , and is not shown in Table 5.12.

Table 5.12 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations between ostrich skin and neckline traits from a six-trait analysis, excluding live weight as covariate

Trait	CSS	NLTL	NLCL	NLWT	NLWM	NLA
<i>Additive genetic correlations (h^2 in bold)</i>						
CSS	0.21 ± 0.07	0.54 ± 0.16	0.43 ± 0.18	0.13 ± 0.18	0.27 ± 0.22	0.29 ± 0.18
NLTL		0.27 ± 0.06	0.86 ± 0.05	0.31 ± 0.16	0.56 ± 0.16	0.62 ± 0.11
NLCL			0.22 ± 0.06	0.01 ± 0.18	0.71 ± 0.15	0.41 ± 0.15
NLWT				0.29 ± 0.06	0.24 ± 0.19	0.91 ± 0.03
NLWM					0.17 ± 0.05	0.51 ± 0.16
NLA						0.26 ± 0.06
<i>Residual correlations (σ_e^2 in bold)</i>						
CSS	67	0.37 ± 0.04	0.29 ± 0.04	0.27 ± 0.05	0.12 ± 0.05	0.34 ± 0.05
NLTL		2057	0.79 ± 0.02	0.18 ± 0.05	0.21 ± 0.05	0.50 ± 0.04
NLCL			1618	0.13 ± 0.05	0.17 ± 0.05	0.55 ± 0.04
NLWT				29	0.16 ± 0.05	0.90 ± 0.01
NLWM					14	0.21 ± 0.04
NLA						0.024
<i>Phenotypic correlations (σ_p^2 in bold)</i>						
CSS	92	0.40 ± 0.03	0.31 ± 0.03	0.22 ± 0.03	0.14 ± 0.03	0.32 ± 0.03
NLTL		2810	0.81 ± 0.01	0.22 ± 0.03	0.28 ± 0.03	0.53 ± 0.02
NLCL			2079	0.10 ± 0.03	0.28 ± 0.03	0.51 ± 0.02
NLWT				42	0.18 ± 0.03	0.90 ± 0.01
NLWM					17	0.27 ± 0.03
NLA						0.033

^a CSS: crust skin size; NLTL: Neckline total length; NLCL: Neckline length in crown; NLWT: Neckline width at top of crown; NLWM: Neckline width in middle of crown; NLA: Neckline area in crown

When live weight was included as a covariate in the multi-trait analysis of crust skin size and neckline traits, the estimate of pe^2 for crust skin size became insignificant at 0.00 ± 0.02 and was consequently excluded, based on the lack of improvement of the log-likelihood. Final results from a multi-trait model including live weight as a linear covariate are reported in Table 5.13.

The heritability of crust skin size and the genetic correlations involving crust skin size were much lower than in the analysis without live weight as a covariate. However, the heritability estimates for the neckline traits and the genetic, residual and phenotypic correlations among neckline traits remained largely unchanged.

Since no effect of the covariate on these traits was found, no further analysis (involving post mortem weight or crust skin size as covariate) was attempted.

Table 5.13 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations between ostrich skin and neckline traits from a six-trait analysis, including live weight as covariate

Trait ^a	CSS	NLTL	NLCL	NLWT	NLWM	NLA
<i>Additive genetic correlations (h^2 in bold)</i>						
CSS	0.14 \pm 0.04	0.11 \pm 0.20	0.08 \pm 0.21	-0.14 \pm 0.19	0.01 \pm 0.23	-0.08 \pm 0.20
NLTL		0.25 \pm 0.06	0.83 \pm 0.06	0.30 \pm 0.16	0.55 \pm 0.16	0.59 \pm 0.12
NLCL			0.21 \pm 0.06	-0.03 \pm 0.18	0.69 \pm 0.15	0.36 \pm 0.16
NLWT				0.31 \pm 0.07	0.24 \pm 0.19	0.92 \pm 0.03
NLWM					0.17 \pm 0.05	0.50 \pm 0.16
NLA						0.28 \pm 0.06
<i>Residual correlations (σ^2_e in bold)</i>						
CSS	36	0.28 \pm 0.04	0.20 \pm 0.04	0.16 \pm 0.05	0.08 \pm 0.04	0.22 \pm 0.05
NLTL		1893	0.78 \pm 0.02	0.11 \pm 0.05	0.18 \pm 0.05	0.45 \pm 0.04
NLCL			1523	0.08 \pm 0.05	0.15 \pm 0.05	0.51 \pm 0.04
NLWT				27	0.14 \pm 0.05	0.89 \pm 0.01
NLWM					14	0.18 \pm 0.05
NLA						0.022
<i>Phenotypic correlations (σ^2_p in bold)</i>						
CSS	42	0.25 \pm 0.03	0.18 \pm 0.03	0.10 \pm 0.03	0.07 \pm 0.03	0.15 \pm 0.03
NLTL		2532	0.79 \pm 0.01	0.16 \pm 0.03	0.26 \pm 0.03	0.48 \pm 0.02
NLCL			1932	0.05 \pm 0.03	0.26 \pm 0.03	0.47 \pm 0.02
NLWT				40	0.16 \pm 0.03	0.90 \pm 0.01
NLWM					17	0.25 \pm 0.03
NLA						0.030

^a CSS: crust skin size; NLTL: Neckline total length; NLCL: Neckline length in crown; NLWT: Neckline width at top of crown; NLWM: Neckline width in middle of crown; NLA: Neckline area in crown

5.4 Discussion

5.4.1 Descriptive statistics

Means and standard deviations for crown and neckline traits were similar to those previously reported by Engelbrecht *et al.* (2007), despite the much lower mean age (322 ± 111 days) of the ostriches used in the study. This confirms the result reported in Table 5.2 that age on its own, or in interactions with other effects did not have a big influence on many of these traits, and on the neckline traits in particular.

The high coefficients of variation for traits such as live weight could be attributed in part to the wide range of ages at which the ostriches were slaughtered. Data from slaughter birds aged 14 months had a much lower coefficient of variation of approximately 12% for *post mortem* weight (Cloete *et al.*, 2002).

Measuring and evaluation methods probably also contributed to the high variation found for many of the slaughter and skin traits. leather thickness, especially, is highly dependent on the exact location on the skin where the measurements are taken, as well as the processing batch as influenced by slaughter group, because the thickness is influenced by the flaying and processing methods used in that particular area for that specific batch.

Processing of the leather could not be standardized because the ostriches were slaughtered over a period of 12 years. Processing methods were constantly changed and improved during this period. This would also influence crust skin weight, which had a coefficient of variation of 23%. Skin grading were the most variable (44 – 50%), however, not being a continuous trait and possibly reflecting the wide range of grades allocated to the different skins.

5.4.2 Fixed effects

All traits except grading and neckline traits were age-dependent. Engelbrecht *et al.* (2007) previously found an age effect for neckline length in the crown and neckline width at the top, though, when skins over a wider age range were evaluated. The increase of ostrich live weight, skin size and leather thickness with an increased slaughter age is well documented (Angel *et al.*, 1997; Cloete *et al.*, 1998; 2004; Meyer *et al.*, 2002; Engelbrecht *et al.*, 2005; 2007; Bhiya, 2006; Van Schalkwyk, 2008).

The effect of gender on leather thickness was consistent with results reported by Van Schalkwyk *et al.* (2002) and Cloete *et al.* (2004), where leather thickness was measured in the crown area of the skin, and the previous finding of Engelbrecht *et al.* (2005). Anderson *et al.* (1991) reported similar gender differences in pelts of lambs, with rams having thicker pelts than wethers.

Processed male skins were accordingly heavier than skins from female ostriches, despite skin size not being influenced by gender. This is consistent with previous reports that the average fat-free raw skin weight of male ostriches was heavier than that of female ostriches (Meyer *et al.*, 2002).

These results are consistent with previous work that indicated that ostriches do not exhibit the same degree of gender differentiation as many other domesticated species (Cloete *et al.*, 2002). Various previous studies indicated that both bodyweight and skin yield (area) were not influenced by gender (Cloete *et al.*, 1998; Meyer *et al.*, 2002; Engelbrecht *et al.*, 2005).

While the fixed, covariate and interaction effects accounted for between 33 and 64% of the variation in most slaughter, skin (with the exception of skin grading) and crown traits, it only explained between 8 and 15% of

the variation in neckline traits. This indicates that neckline traits were less dependent on factors such as age, gender and contemporary group effects than the other skin traits.

5.4.3 (Co)variance components, ratios and correlations

5.4.3.1 Slaughter traits

Usable genetic variation was demonstrated in single-trait analysis for all skin traits, with the exception of skin grading, for which no genetic variation were found. Skin grading, as determined by skin damage, is known to be predominantly affected by behaviour and the environment at farm level where the ostriches are raised (Meyer *et al.*, 2002; MacNamara *et al.*, 2003; Meyer, 2003), so this result was not entirely unexpected.

The h^2 estimate for live weight (0.24 in multi-trait analysis) was similar to previous estimates of 0.32 (Meyer *et al.*, 2002) and 0.28 (Bunter & Cloete, 2004), but lower than the 0.46 reported by Engelbrecht *et al.* (2005). The h^2 estimates of crust skin size (between 0.19 and 0.23 in the various analyses) were also similar to the previous estimate of 0.21 (Meyer *et al.*, 2002).

Positive genetic correlations of live weight with crust skin size and crust skin weight indicate that indirect selection for these skin traits would be possible by selection for live weight. However, the improvement in the heritability estimate for crust skin weight when live weight was accounted for indicates that the genetic variation in skin weight was independent of body weight.

Despite the moderate h^2 of leather thickness, which were also independent of live weight, leather thickness was only related to crust skin weight, both on a genetic and phenotypic level. The insignificant correlations of leather thickness with live weight and crust skin size indicate that leather thickness (as defined in the present genetic resource) would not be influenced by selection for weight.

5.4.3.2 Crown traits

Similar heritability estimates for crown traits were found in single- and multi-trait analyses. The heritability of crown length was not significant, while the rest of the crown traits had low to moderate h^2 estimates. When live weight was included as a covariate, all the heritability estimates were significantly reduced, with only crown shape remaining significantly heritable. This is in contrast to a previous study by Engelbrecht *et al.* (2007) where the heritability of crown width and crown length remained significant after inclusion of weight as a covariate in the model. This result could be related to the narrower age and weight range of the data used during this study.

While most of the genetic correlations between the crust skin size and crown traits become insignificant when live weight were accounted for, the genetic correlation between crust skin size and crown size remained high and significant. This finding suggested that crown size did not depend exclusively on size

differences between animals. However, selection for skins with a higher percentage of nodulated skin is not likely to be straightforward, as the genetic variation in crown size was substantially reduced after size differences were accounted for by including live weight as a covariate in the analysis (see Tables 5.8 and 5.9).

Maternal effects were important for crown width only. The maternal effect was significant for crust skin size when analysed with skin traits, but became insignificant when analysed together with crown traits, including live weight as covariate (0.01 ± 0.02).

5.4.3.3 Neckline traits

Live weight was positively correlated on the genetic level with neckline length and neckline size in two-trait analyses between live weight and these traits. Genetic correlations of crust skin size with total neckline length and neckline length in the crown were insignificant in multi-trait analysis. The inclusion of live weight as covariate also did not influence the h^2 estimates and genetic correlations involving neckline traits to the same extent as it did with the crown traits. The results seem to suggest that the width and size of the neckline were not as dependent on the size of the animal as the length of the neckline.

These results are in agreement with what Engelbrecht *et al.* (2007) reported earlier. Heritability estimates for neckline traits remained moderate after scaled for size differences by the inclusion of live weight as a covariate (see Table 5.12). This result, as well as the absence of a significant genetic correlation of neckline size (when scaled for live weight) with crust skin size seem to suggest that neckline size may be changed independently from live weight by genetic selection. This result should possibly be explored further in subsequent research. The contribution of a change in neckline traits to the economic production of ostrich leather should also be ascertained.

Overall, there was no indication of any serious unfavourable genetic correlations among slaughter, skin, crown and neckline traits. The high standard errors associated with some of the correlations make it difficult to draw reliable conclusions, though. More data are thus needed to verify some of these findings.

5.5 Conclusions

Results from the present study clearly suggest that most skin and crown traits were influenced by age, suggesting that producers may obtain higher yields for some of the quantitative skin traits at higher ages. Despite this, it was demonstrated that significant genetic variation in most quantitative skin traits (such as crust skin size, crust skin weight, leather thickness and neckline traits) persisted, even after the effects of age and subsequently live weight were accounted for. Moderate estimates of heritability for these traits, combined with moderate to high levels of phenotypic variation, therefore indicate that these traits will respond to selection. Genetic correlations of slaughter traits (live weight and crust skin size) with quantitative

(crown size) and qualitative (neckline size) traits were also mostly favourable or negligible. Sustained genetic progress in these traits thus seems to be feasible. These traits can thus potentially be considered in a selection program for ostriches, depending on their economic value in real terms.

5.6 References

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CHAPTER 6

Estimation of environmental and genetic factors influencing subjectively assessed ostrich leather traits

6.1 Introduction

Ostrich leather is considered unique due to the feather follicles which gives it a distinctive nodulated appearance (Engelbrecht *et al.*, 2009). The appearance of these nodules is consequently important when the value of ostrich leather is determined (Engelbrecht *et al.*, 2005). Despite its importance, nodule traits are assessed subjectively owing to a lack of practical objective evaluation methods (Van Schalkwyk *et al.*, 2005; Cloete *et al.*, 2006). A subjective score is generally assigned to each skin based on the overall nodule development as perceived by the specific grader. However, the appearance and distribution of nodules varies between different locations on the skin (Cloete *et al.*, 2006), making it difficult to accurately and objectively evaluate overall nodule development.

Other aspects that influence the value of ostrich leather that are also being assessed subjectively are skin damage and skin defects. The occurrence of hair follicles among the feather follicles is seen as one such defect and is also subjectively assessed as part of skin grading. The excessive occurrence of hair follicles results in skins being downgraded (Lunam & Weir, 2006) and it is therefore also an economically important trait.

Meyer *et al.* (2004) reported low heritabilities for nodule traits when measured with objective methods, while Engelbrecht *et al.* (2005; 2009) subsequently reported significantly higher heritability estimates for these traits when analysing subjective scores for the traits.

Data regarding skin traits such as nodule characteristics are generally difficult to acquire because of a lack of objective evaluation procedures. It was clear, however, that by assigning scores to these quality traits it was possible to estimate plausible genetic parameters for these traits (Engelbrecht *et al.*, 2005; 2009). The data was consequently recently updated to include more recent information on the full resource of available chrome-crusted skins for the estimation of genetic and environmental parameters for various qualitative skin traits. The results will be used to investigate the possibility of improving these subjectively assessed leather traits through genetic selection.

6.2 Materials and methods

6.2.1 Data description

Pedigree and slaughter data were obtained from the ostrich breeding flock maintained at the Oudtshoorn Research Farm, South Africa, as described in Chapters 2, 3 and 5. Ostriches were weighed on the farm, either before pre-slaughter isolation (approximately 14 days before slaughter) or before transportation to the abattoir (1 day before slaughter), to obtain a pre-slaughter live weight. The age at weighing was recorded in all instances. The ostriches were slaughtered and dressed at an abattoir approved by the European Union, as described in Chapter 3. *Post mortem* weight was recorded at the abattoir after the ostriches were stunned and bled out. *Post mortem* weight was only recorded from 2001 onwards.

The skins of the slaughter ostriches were processed and chrome-crusted according to standard procedures (Meyer, 2003). The chrome-crusted skins were evaluated and subjective scores assigned to nodule traits (size, shape and distribution) and hair follicle prevalence. The scoring system was devised and consistently applied to the available resource of skins by the same scorer, namely the author herself to exclude the possibility of variation between scorers.

Average nodule size and nodule shape on skins were evaluated on linear scales of 1 to 9, with one indicating poor quality and 9 indicating excellent quality. Scores were subjectively assigned to each skin based on the overall or average size and shape of the nodules on the skin.

Scoring for nodule size was standardized by establishing visual standards for each score. A representative skin was chosen to represent each score from one to nine based on the average size of the nodules on the skin. These skins served as standards against which each skin could be compared during scoring. A score of five represented average-sized nodules, one referred to very small nodules (poor) and nine to very big nodules (excellent).

For nodule shape, each score was defined in terms of the general shape of the nodules on the skin. Scores of 1 to 3 were used for skins with mostly poorly developed or elongated nodules, 4 to 6 for skins with mostly relatively rounded nodules and 7 to 9 for skins with mostly well-rounded nodules. Each skin was scored according to these definitions:

Poor: 1 – Large areas of poorly defined, distinctly elongated and open nodules
2 – Many elongated nodules or poorly developed nodules
3 – Relatively poorly developed or open, elongated nodules

Average: 4 – Relatively rounded nodules with many open or elongated nodules
5 – Relatively rounded with some open nodules

6 – Relatively rounded with mostly closed nodules

Good: 7 – Mostly rounded nodules with some open or poorly developed nodules

8 – Rounded, closed nodules with a flat shape

9 – Well-defined, well-rounded closed nodules

Nodule distribution was scored on a linear scale of one to five, considering the overall distribution of the nodules on a skin pertaining to size, shape and distance between nodules. A score of five represented a skin where the size, shape and distance between nodules were uniform across the whole crown area, while a score of one would be a skin where the nodules were very poorly distributed, with the size, shape and distance between nodules varying substantially between different locations on the skin.

The overall occurrence of hair follicles on each skin was also scored on a scale of one to nine, with one indicating no hair follicles and nine the excessive occurrence of hair follicles on the whole skin.

6.2.2 Statistical analysis

The ASReml programme (Gilmour *et al.*, 2009) was used for estimation of fixed effects and subsequently to derive variance components for the respective slaughter and skin traits in single-trait analysis.

Fixed effects considered included contemporary group, as described in Chapter 2 (for pre-slaughter live weight), or slaughter group (for slaughter and skin traits), and gender (male or female). Slaughter age was included as a linear covariate for all slaughter and skin traits, while age at weighing was included as a linear covariate for pre-slaughter live weight.

The first analyses involved fitting various combinations of fixed effects and interactions between them to obtain an operational model. Effects found to be significant ($P < 0.05$) in preliminary analyses were retained in subsequent analyses.

Random effects were then added sequentially to the operational model. Direct additive genetic effects and maternal permanent environmental effects were modelled for each trait. Maternal permanent environmental effects were also fitted per dam year because the majority of dams had data of progeny hatched in more than one year recorded. The full linear mixed model (in matrix notation) fitted for each trait was as follows:

$$y = X\beta + Z_1a + Z_2pe + Z_3w + e$$

where y was a vector of observations for the respective slaughter or skin traits; β , a , pe and w were vectors of fixed effects, direct genetic, maternal permanent environmental and within year permanent environmental effects, respectively; X , Z_1 , Z_2 and Z_3 are the corresponding incidence matrices relating the respective effects to y ; and e is the vector of residuals. It was assumed that:

$$V(a) = A\sigma_a^2; V(pe) = I\sigma_{pe}^2; V(w) = I\sigma_w^2 \text{ and } V(e) = I\sigma_e^2,$$

where A was the numerator relationship matrix, I was an identity matrix and σ_a^2 , σ_{pe}^2 , σ_w^2 and σ_e^2 were the direct genetic variance, maternal permanent environmental variance, within year permanent environmental variance and environmental (residual) variance, respectively.

Log-likelihood tests were conducted to determine the most suitable random effects model. Subsequently, multi-trait animal models were fitted for calculation of all relevant direct additive genetic and environmental correlations between traits, together with their appropriate standard errors. Initially pre-slaughter live weight was analysed with *post mortem* weight and with each individual subjectively assessed trait, respectively, in five two-trait analyses.

A six-trait analysis involving pre-slaughter live weight, crust skin size and all subjective traits was subsequently conducted. This was followed by a five-trait analysis, where pre-slaughter live weight was included as a linear covariate to account for the effect of size. The latter analyses were repeated replacing pre-slaughter live weight with *post mortem* weight. Lastly, a four-trait analysis was done, using crust skin size as a linear covariate to account for the effect of size independently from weight.

All analyses included the full pedigree file, consisting of 6 541 individuals, the progeny of 380 sires and 379 dams, mated to each other in 543 unique combinations.

6.3 Results

6.3.1 Descriptive statistics

Processed crust skins from birds slaughtered between 1997 and 2012, aged between 210 and 540 days, were scored for nodule traits (nodule size, nodule shape and nodule distribution), and for the prevalence of hair follicles. Forty six skins, representing a wide range of subjective scores, were scored twice to check for consistency. The correlations between repeated scores for the same skin amounted to 0.92, 0.79, 0.51 and 0.44 for nodule size, nodule shape, nodule distribution and hair follicle score, respectively.

The final dataset analysed only included ostriches slaughtered from 2001 onwards, however, due to the availability of data for *post mortem* weight. This dataset consisted of 1 125 records, of which 950 were slaughter ostriches and 175 were breeder birds with comparable live weight records, representing the progeny of 218 sires and 212 dams, mated to each other in 258 unique combinations. The average slaughter age (\pm s.d.) of these ostriches were 404 ± 52 days (ranging from 294 to 540 days of age) and the number of records ranged between 913 and 1 125 for the various traits (Table 6.1).

Nodule trait scores had moderate coefficients of variation (CV). The CV for hair follicle prevalence was higher, while crust skin size had a low CV. The distribution of scores for nodule traits and hair follicles did not deviate from normality. Shapiro-Wilk statistics ranged between 0.83 for nodule distribution score and 0.95 for hair follicle score.

Table 6.1 Characteristics of the data for ostrich slaughter and subjectively scored skin quality traits

Trait	N	Mean \pm s.d.	CV (%)	Range
Pre-slaughter live weight (kg)	1125	93.9 \pm 16.7	18	40 - 148
<i>Post mortem</i> weight (kg)	950	84.0 \pm 14.4	17	34.3 – 134.7
Crust skin size (dm ²)	950	141 \pm 12	9	78 - 178
Nodule size score (1-9)	950	4.4 \pm 1.1	25	1-9
Nodule shape score (1-9)	950	4.1 \pm 1.2	29	1-8
Nodule distribution score (1-5)	913	2.8 \pm 0.7	25	1-5
Hair follicle score (1-9)	950	3.9 \pm 1.7	44	1-9

N: number of records; s.d.: standard deviation; CV: coefficient of variation

6.3.2 Fixed effects

Significance levels for fixed effects ($P < 0.05$) for each trait are presented in Table 6.2.

Table 6.2 Significant^a fixed effects influencing slaughter and skin traits

Trait	Contemporary		Gender	Age x		R ²	
	Age	group (CG)	(G)	CG	Age x G		G x CG
Pre-slaughter live weight ^b	***	***	n.s.	***	n.s.	n.s.	0.45
<i>Post mortem</i> weight	**	***	n.s.	*	n.s.	n.s.	0.43
Crust skin size	***	***	n.s.	***	n.s.	n.s.	0.32
Nodule size score	***	***	***	n.s.	n.s.	n.s.	0.16
Nodule shape score	*	***	***	n.s.	n.s.	n.s.	0.10
Nodule distribution score	n.s.	***	**	n.s.	n.s.	*	0.03
Hair follicle score	**	***	***	n.s.	n.s.	n.s.	0.22

^a Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s.: not significant

^b For pre-slaughter live weight, age refers to age at last live weighing and contemporary group refers to rearing group, while for the rest of the traits, age refers to slaughter age and contemporary group to slaughter group

Scores for all traits increased with age, with the exception of nodule distribution, which was not affected by age. Scores for nodule size, nodule shape and the prevalence of hair follicles increased by 0.004 ± 0.002 , 0.003 ± 0.002 and 0.006 ± 0.002 , respectively for each day increase in age.

Contemporary group affected all traits ($P < 0.001$), while gender only influenced the qualitative skin traits. Means for the skin quality scores as influenced by gender are given in Table 6.3. Males had higher scores for all the nodule traits as well as for hair follicle score.

Table 6.3 Least squares means (\pm s.e.) for subjectively assessed skin quality traits as influenced by gender

Trait	Male	Female
Nodule size score	4.64 \pm 0.05	4.39 \pm 0.05
Nodule shape score	4.39 \pm 0.06	4.10 \pm 0.06
Nodule distribution score	2.86 \pm 0.03	2.73 \pm 0.03
Hair follicle score	3.79 \pm 0.08	3.25 \pm 0.08

6.3.3 (Co)variance components, ratios and correlations

Log-likelihood values under alternative models for random effects are presented for each trait in Table 6.4. For all traits, the inclusion of the direct genetic component as a random effect in the operational model resulted in an improved log-likelihood when compared to basic fixed effect models. No further significant improvement was obtained by adding other random effects. The random effect of animal was consequently retained for all traits in the multi-trait models.

Table 6.4 Log-likelihood (LogL) values for models^a fitting different random effects for ostrich slaughter and skin traits in single-trait animal model analysis. The best model is denoted in bold

Trait	Models				
	FE	FE + h ²	FE + h ² + pe ²	FE + h ² + pe ² .yr	FE + h ² + pe ² + pe ² .yr
Pre-slaughter live weight	-3411.50	-3362.98	-3361.62	-3362.08	-3361.24
Post mortem weight	-2740.07	-2694.01	-2693.44	-2694.01	-2693.44
Crust skin size	-2628.35	-2574.30	-2573.04	-2574.25	-2573.04
Nodule size score	-547.195	-513.531	-513.531	-512.836	-512.836
Nodule shape score	-621.179	-589.677	-589.677	-589.677	-589.677
Nodule distribution score	-164.402	-153.545	-153.017	-153.097	-152.660
Hair follicle score	-895.541	-849.383	-848.787	-849.342	-848.787

^a FE = fixed effects only; FE + h² = FE + animal effect (A); FE + h² + pe² = FE + A + permanent environment of dam (dam_{pe}); FE + h² + pe² + pe².yr = FE + A + dam_{pe} + maternal permanent environment within year (dam_{pe}.yr)

Estimates of genetic parameters from single-trait analyses are presented in Table 6.5. Heritability was estimated at between 0.26 (nodule distribution) and 0.50 (hair follicles) for the respective traits in single-trait analyses.

Genetic correlations between pre-slaughter live weight and the nodule traits were all positive, although the correlations with nodule shape and nodule distribution scores were not significantly different from zero (Table 6.6). The genetic correlation between live weight and hair follicle score was negative, but was also not significantly different to zero.

Environmental and phenotypic correlations with live weight were comparable in sign and magnitude for two-trait analyses involving *post mortem* weight, nodule size score and nodule shape score. In the case of nodule distribution score, environmental and phenotypic correlations were comparable in sign but smaller in

magnitude when compared to the genetic correlation. The environmental correlation involving live weight and hair follicle score was positive, in contrast to the genetic correlation that was negative in sign.

Table 6.5 (Co)variance components and ratios^a (\pm s.e.) for ostrich slaughter and skin traits estimated from single-trait analyses

Trait ^b	h^2	σ^2_a	σ^2_e	σ^2_p
LW	0.45 \pm 0.08	72.1	89.2	161.3
PMW	0.49 \pm 0.09	60.4	62.3	122.7
CSS	0.49 \pm 0.09	50.8	52.4	103.1
NSZ	0.35 \pm 0.08	0.376	0.705	1.082
NS	0.36 \pm 0.08	0.468	0.816	1.285
ND	0.26 \pm 0.08	0.130	0.364	0.493
HF	0.49 \pm 0.09	1.155	1.217	2.372

^a h^2 : direct heritability; σ^2_a : direct additive variance; σ^2_e : residual variance; σ^2_p : total phenotypic variance

^b LW: live weight; PMW: *post mortem* weight; CSS: crust skin size; NSZ: nodule size score; NS: nodule shape score; ND: nodule distribution score; HF: hair follicle score

Table 6.6 Estimates of genetic (r_g), environmental (r_e) and phenotypic (r_p) correlations (\pm s.e.) among ostrich slaughter and skin traits from two-trait models

Trait	Correlated trait	r_g	r_e	r_p
Live weight	Crust skin size	0.94 \pm 0.03	0.66 \pm 0.04	0.78 \pm 0.01
	<i>Post mortem</i> weight	0.99 \pm 0.01	0.82 \pm 0.02	0.88 \pm 0.01
	Nodule size score	0.41 \pm 0.14	0.41 \pm 0.08	0.41 \pm 0.03
	Nodule shape score	0.11 \pm 0.17	0.19 \pm 0.09	0.15 \pm 0.04
	Nodule distribution score	0.19 \pm 0.18	0.04 \pm 0.08	0.09 \pm 0.04
	Hair follicle score	-0.19 \pm 0.15	0.23 \pm 0.11	0.02 \pm 0.04

Results of a six-trait analysis including pre-slaughter live weight, crust skin size and all the subjectively assessed skin traits are shown in Table 6.7. Heritability estimates were similar to those obtained in single-trait analysis. The genetic, environmental and phenotypic correlations were also comparable in sign and magnitude to those between pre-slaughter live weight and the other traits reported in Table 6.6.

Apart from the correlations involving pre-slaughter live weight, significant genetic correlations also occurred between crust skin size and nodule size (0.51), crust skin size and nodule shape (0.39), nodule size and nodule shape (0.72) and nodule shape and nodule distribution (0.52). Phenotypic and residual correlations among the objective traits and the nodule traits were generally positive, and mostly smaller in magnitude than the corresponding genetic correlation.

Correlations involving hair follicle score were not as predictable, the sign of environmental correlations involving pre-slaughter live weight and crust skin size (positive) being different to that of the corresponding genetic correlations (negative). These results are consistent with those reported in Table 6.6 in the case of pre-slaughter live weight.

Table 6.7 (Co)variance components and ratios (\pm s.e.), along with residual and phenotypic variances and correlations for ostrich slaughter and subjective skin traits as estimated in multi-trait analyses

Trait ^a	LW	CSS	NSZ	NS	ND	HF
<i>Additive genetic correlations (h^2 in bold on diagonal)</i>						
LW	0.48 \pm 0.09	0.94 \pm 0.03	0.37 \pm 0.15	0.16 \pm 0.17	0.20 \pm 0.18	-0.17 \pm 0.15
CSS		0.51 \pm 0.09	0.51 \pm 0.12	0.39 \pm 0.15	0.27 \pm 0.17	-0.26 \pm 0.15
NSZ			0.34 \pm 0.08	0.72 \pm 0.10	0.28 \pm 0.18	0.08 \pm 0.17
NS				0.37 \pm 0.08	0.52 \pm 0.15	0.01 \pm 0.17
ND					0.28 \pm 0.08	-0.10 \pm 0.18
HF						0.50 \pm 0.09
<i>Residual correlations (σ_e^2 in bold on diagonal)</i>						
LW	95.0	0.64 \pm 0.05	0.44 \pm 0.07	0.17 \pm 0.09	0.04 \pm 0.08	0.22 \pm 0.10
CSS		54.4	0.49 \pm 0.07	0.11 \pm 0.09	0.02 \pm 0.08	0.25 \pm 0.11
NSZ			0.730	0.40 \pm 0.06	0.21 \pm 0.07	0.12 \pm 0.08
NS				0.812	0.29 \pm 0.07	0.09 \pm 0.09
ND					0.359	0.04 \pm 0.08
HF						1.202
<i>Phenotypic correlations (σ_p^2 in bold on diagonal)</i>						
LW	183	0.79 \pm 0.01	0.40 \pm 0.03	0.16 \pm 0.04	0.10 \pm 0.04	0.03 \pm 0.04
CSS		111	0.49 \pm 0.03	0.23 \pm 0.04	0.11 \pm 0.04	-0.00 \pm 0.04
NSZ			1.10	0.51 \pm 0.03	0.23 \pm 0.04	0.11 \pm 0.04
NS				1.29	0.36 \pm 0.03	0.05 \pm 0.04
ND					0.50	-0.01 \pm 0.04
HF						2.38

^a LW: live weight; CSS: crust skin size; NSZ: nodule size score; NS: nodule shape score; ND: nodule distribution score; HF: hair follicle score

Estimates of heritability (h^2) for the subjectively assessed skin traits as obtained from various multi-trait analyses, with and without taking size into account (as reflected by live weight, *post mortem* weight and crust skin size) as linear covariates, are provided in Table 6.8.

Table 6.8 Heritability estimates for subjectively assessed ostrich skin traits as estimated in various multi-trait analyses, with or without size as a linear covariate

Trait ^a	Linear covariate fitted			
	none	LW	PSW	CSS
NSZ	0.34 \pm 0.08	0.35 \pm 0.08	0.35 \pm 0.08	0.34 \pm 0.08
NS	0.37 \pm 0.08	0.37 \pm 0.08	0.36 \pm 0.08	0.33 \pm 0.08
ND	0.28 \pm 0.08	0.27 \pm 0.08	0.28 \pm 0.08	0.27 \pm 0.08
HF	0.50 \pm 0.09	0.51 \pm 0.09	0.51 \pm 0.09	0.50 \pm 0.09

^a LW: live weight; PMW: *post mortem* weight; CSS: crust skin size; NSZ: nodule size score; NS: nodule shape score; ND: nodule distribution score; HF: hair follicle score

Size, when accounted for by adding pre-slaughter live weight, *post mortem* weight or crust skin size as linear covariate to the model, evidently did not significantly influence the estimates of heritability for nodule traits and hair follicle prevalence. Heritability estimates were consistent across different sets of analyses.

The genetic and phenotypic correlations between the subjectively assessed ostrich skin traits as estimated in various multi-trait models are given in Table 6.9. Mostly similar values were obtained for all correlations when analysed with the different models, regardless of the inclusion of live weight or crust skin size as linear covariate or not. All these results indicated that nodule size and nodule shape was genetically correlated, as was nodule shape and nodule distribution. No other genetic correlations were significant.

Table 6.9 Genetic and phenotypic correlations for subjectively assessed ostrich skin traits as estimated in various multi-trait analyses, with or without pre-slaughter live weight or crust skin size as a linear covariate

Trait ^a	Correlated trait	Without LW / CSS		With LW		With CSS	
		r _g	r _p	r _g	r _p	r _g	r _p
NSZ	NS	0.72 ± 0.10	0.51 ± 0.03	0.71 ± 0.10	0.49 ± 0.03	0.62 ± 0.13	0.47 ± 0.03
	ND	0.26 ± 0.18	0.23 ± 0.04	0.22 ± 0.19	0.21 ± 0.04	0.15 ± 0.19	0.20 ± 0.04
	HF	0.07 ± 0.17	0.10 ± 0.04	0.18 ± 0.16	0.10 ± 0.04	0.28 ± 0.16	0.13 ± 0.04
NS	ND	0.53 ± 0.15	0.36 ± 0.03	0.52 ± 0.15	0.35 ± 0.03	0.49 ± 0.16	0.35 ± 0.03
	HF	0.01 ± 0.17	0.05 ± 0.04	0.03 ± 0.17	0.05 ± 0.04	0.07 ± 0.17	0.05 ± 0.04
ND	HF	-0.11 ± 0.18	-0.02 ± 0.04	-0.09 ± 0.18	-0.02 ± 0.04	-0.07 ± 0.18	-0.01 ± 0.04

^a LW: live weight; CSS: crust skin size; NSZ: nodule size score; NS: nodule shape score; ND: nodule distribution score; HF: hair follicle score

6.4 Discussion

6.4.1 Descriptive statistics

Lower coefficients of variation for nodule size and nodule shape scores were obtained in the present study, when compared to a preliminary study by Engelbrecht *et al.* (2005). Although the number of records was similar, the records used during this study came from a more representative, narrower slaughter age range compared to the age range of 126 to 506 days of the ostriches used in the earlier study. The coefficient of variation for hair follicle score was similar though, possibly indicating that the variation in hair follicle scores was not as dependent on age.

The variation in nodule size reported when measured objectively were 15.2% (Meyer *et al.*, 2004), compared to the coefficient of variation of 25% found when evaluated subjectively during this study. Measurements in above-mentioned study were only done in five predetermined locations on the skin, however, while the subjective score assigned during this study were for the entire nodulated area. Large within skin variation complicates the scoring of a skin as one unit, probably contributing to the larger variation found when scored

subjectively. The scoring system used during this study was specifically devised to improve consistency, however, following previously inconsistent assessments of ostrich skins where prior standardization of the linear scale was not attempted (see Van Schalkwyk *et al.*, 2005). The lack of consistency between mean scores of individual scorers (reflected by a between scorer variance ratio of 35%) found during the study by Van Schalkwyk *et al.* (2005), was addressed by having the same scorer evaluate all skins in the present study. Scoring for nodule size and nodule shape was found to be relatively consistent in skins that were evaluated on two occasions, while scoring for nodule distribution was not as consistent. The complexity of the trait definition, as well as a clear definition of what nodule distribution entails, probably made accurate scoring difficult. The trait definition actually takes into account three different aspects, namely the distribution of the size, shape and distance between nodules, which should possibly rather each be scored individually. Scoring traits individually rather than in combination increases the accuracy of linear scores so derived (Olivier *et al.*, 1987). Scoring for hair follicles was also not very consistent, possibly due to the wider range of scores used. It also had a high coefficient of variation of 44%. A smaller range of scores can be considered for future use in scoring this trait.

6.4.2 *Fixed effects*

Identifiable fixed effects overall explained relatively little variation in subjectively assessed nodule traits. While the variation in pre-slaughter live weight and *post mortem* weight was relatively well described by factors such as contemporary group, along with age at recording, these factors failed to explain the variation in subjective scores for nodule traits and hair follicles. Nonetheless, contemporary group and gender effects were significant for all the subjectively scored traits, although the percentage of variance accounted for was comparatively low. Scores for nodule size, nodule shape and hair follicles increased with age. Engelbrecht *et al.* (2005) reported similar increases with age for nodule size and nodule shape, but did not find an increase in hair follicle score with age.

Males generally had higher scores than females for all the subjectively scored traits. This is in agreement with an earlier report by Engelbrecht *et al.* (2005) for nodule size and nodule shape. Although Engelbrecht *et al.* (2005) did not find a significant difference between males and females for hair follicle score, males also had higher absolute scores for hair follicles. The standard errors associated with these values were higher than the ones reported in this study though, resulting in these differences not being significant. This is understandable if the age range in the two studies is considered.

6.4.3 *(Co)variance components, ratios and correlations*

The single-trait heritability estimates were moderate to high for all traits analysed and compared well with the multi-trait estimates. Estimates for nodule size score were somewhat lower than previously reported by Engelbrecht *et al.* (2005) when data from skins involving a wider slaughter age range were included in a linear model analysis (0.43), while estimates for nodule shape score and hair follicle score were somewhat higher. When compared to estimates obtained by means of threshold model analysis of these subjectively

scored skin traits (Engelbrecht *et al.*, 2009), the results were more comparable, while having smaller standard errors. The heritability estimate of hair follicle score was comparable to that of pinhole (0.40), a similar defect that occurs on lamb pelts (Campbell *et al.*, 1996). Because ostrich skin is unique with regard to its nodulated appearance, no comparable results from other species are available with regard to nodule traits.

The genetic correlation between live weight and post mortem weight did not differ from unity, despite referring to weights taken at different times and recordings of live weight not being standardised to a fixed time before slaughter. The only significant genetic correlations of both measures of live weight and the subjectively assessed skin traits were with nodule size score. This finding is consistent with previous results reported by Engelbrecht *et al.* (2009).

Furthermore, a high genetic correlation was found between scores for nodule size and nodule shape in multi-trait analysis, confirming previous results reported by Engelbrecht *et al.* (2005; 2009). Both nodule size and nodule shape scores were also significantly correlated on a genetic level with crust skin size, while scores for nodule shape and nodule distribution were also significantly correlated. No other significant genetic correlations were found between the slaughter and subjective skin traits investigated, as the standard errors were mostly more than half of the corresponding correlation estimates. It should be noted that the negative direction of the genetic correlation between live weight and hair follicle score in absolute terms is favourable, as selection would strive for a higher live weight and less hair follicles (i.e. lower subjective scores for hair follicles).

Interestingly, accounting for size by including pre-slaughter live weight or crust skin size did not influence the genetic and environmental parameters that were estimated. It is therefore clear that these qualitative skin traits can be improved independently from size or live weight.

6.5 Conclusions

Given its monetary value, the improvement of ostrich leather quality is important for continued profitability in the commercial industry. Accurate evaluation of skin quality and directed genetic selection for improved leather quality are prerequisites for improvement though.

This study demonstrated that sufficient genetic variation exists for nodule traits and hair follicle prevalence to allow sustained genetic progress for these traits, should it be desired as part of the overall selection objective. In practice, selection decisions will depend on progeny test results, as nodule traits cannot be scored on live birds at present. Alternatively, progress in a trait like nodule size could be achieved through indirect selection based on favourable genetic correlations with live weight, evaluated on an age constant basis.

6.6 References

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CHAPTER 7

The combination of slaughter traits in a provisional selection index

When several criteria are employed in the estimation of genetic merit, they may be combined into a single figure known as a selection index, which permit the attainment of maximum genetic progress (Hazel, 1943). Information on growth and the main products (meat and skin) obtained in the ostrich industry will be combined to construct a provisional selection index for slaughter bird production. It needs to be stated that this is by no means an attempt to conduct an exhaustive study into a plausible selection index for slaughter birds. It should rather be seen as a preliminary study of the possible impact of combining a number of traits routinely recorded under present conditions in the South African ostrich industry to assess situations with direct practical application to local farmers.

A selection index is constructed by combining genetic and economic information for various traits that influence an animal's value, as proposed by Hazel (1943). The genetic gain attainable within a group of animals by selection for several traits simultaneously is the product of the selection differential, the correlation between the aggregate breeding value (breeding objective) and the selection index, and genetic variability. According to Hazel (1943), selection for an index which gives a proper weight to each trait is more efficient than selection for one trait at a time or for several traits with an independent culling level for each trait.

The following information is needed to construct a selection index: the phenotypic standard deviations for each trait, the phenotypic and genetic correlation between each pair of traits, the heritability of each trait, and the relative economic value for each trait (Hazel, 1943). The economic value of a trait was defined in this study as the amount by which profit may be expected to change for each unit of improvement in the trait concerned.

It is necessary to gain insight into a selection index that could be considered for improving slaughter traits in ostriches. The MTINDEX Excel spreadsheet for the calculation of selection index calculations (Van der Werf, 2008) was used for preliminary calculations for this purpose. Genetic information was combined with economic information to investigate the impact of a limited number of plausible selection strategies, involving a combination of qualitative and quantitative production traits.

The present payment scheme functions solely on crust skin size, skin grading (see Table 7.1) and nodule development. Skin quality traits like nodule size and nodule shape, as well as hair follicles, exert an important influence on skin grading (Engelbrecht *et al.*, 2009). Skins are downgraded if nodule development, which is collectively determined by nodule size and nodule shape, is found to be unacceptable (with small or

poorly developed nodules). Currently prizes for skins that have unacceptable nodules are significantly lower than for skins with acceptable nodules. A separate, lowered prize table is used for these skins. Skins are also downgraded for the excessive occurrence of hair follicles. The size of the crown and the neckline are not currently considered during the determination of the price of specific skins, even though it will affect the cutting value of a skin. These traits are therefore not considered.

Table 7.1 Table depicting the effect of grade and skin size on the price per square decimetre (dm²) of ostrich skin. Prices are expressed relative to the maximum price attainable, indicated as 100

Crust skin size	Grade 1	Grade 2	Grade 3	Grade 4	Grade 5
>140 dm ²	100	81	76	63	31
130-139 dm ²	97	72	67	59	27
115-129 dm ²	45	43	39	31	17
50-114 dm ²	17	14	13	10	6

Meat income is based solely on carcass weight, with prize per kilogram increasing as carcass weight increases (see Table 7.2). This system of payment is driven by the fact that ostrich meat is mostly marketed as individual muscle cuts, and heavier cuts can be sold at a premium. This holds particularly true in the case of high value cuts like the fan fillet.

Table 7.2 Table depicting the effect of carcass weight on the price per kilogram for ostrich meat. Prices are expressed relative to the maximum price attainable, indicated as 100

Carcass weight (kg)	35	36	37	38	39	40	41	42	43	44	45	46
Relative price	61	69	75	79	81	82	83	84	86	89	93	100

The following traits were consequently included in the index calculations: pre-slaughter live weight (instead of carcass weight for which there was not sufficient data available, and which would not be available for candidate animals for replacement), crust skin size, nodule size score, nodule shape score and hair follicle score. Since these traits were all considered in Chapter 6, the parameters used for the selection index could be derived from Table 6.7.

The economic values were derived by using the mean values reported in Chapters 3 and 6 for the traits as indicative of a typical slaughter ostrich in the resource flock used in this study, combined with current contract price tables (fixed prices over a year period for producers contracted to deliver a pre-determined number of ostriches). Only the direct effect of improvement of one unit in each trait on slaughter income was considered, assuming all other costs to be fixed and not influenced by such an improvement.

It was assumed that nodule size and nodule shape contributed equally to the acceptability of nodule development as assessed by the tannery. The difference in revenue for an average ostrich skin with acceptable versus unacceptable nodules were consequently liberally divided by 9 (for each score) and then divided by two to determine the economic value for each individual trait (nodule size and nodule shape). For

hair follicle score the difference in revenue for an average sized skin being downgraded from grade 2 to grade 3 was also divided by 9 (for each score) to estimate the economic value of one score for hair follicles.

The economic values used were ZAR 12/kg for pre-slaughter live weight (based on and derived from the mean values for pre-slaughter live weight and carcass weight in Table 3.2 and a prize of approximately ZAR 26 per kilogram carcass weight), ZAR 11/dm² for crust skin size (based on the mean crust size in Table 6.1), ZAR 30 for nodule size score, ZAR 30 for nodule shape score and ZAR -13 for hair follicle score. The latter negative weight is due to the fact that the desired outcome in hair follicle score is for a lower score. A similar economic value of ZAR 11/kg for pre-slaughter live weight was previously calculated from a bio-economic model by Cloete *et al.* (2008) for use in a simple preliminary selection index for the industry.

It should be noted though that the meat price is highly reliant on whether the meat is exported fresh or as heat-treated processed products, or alternatively marketed locally. The price used was based on current price predictions for meat being exported as heat-treated processed meat products. Comparable values for meat being marketed locally versus being exported as fresh meat would be in the order of ZAR 8 and ZAR 18, respectively.

It is also difficult to accurately determine the economic value of traits such as nodule shape and nodule score since these collectively determines nodule development, which is assessed subjectively as either acceptable or unacceptable. The economic value calculated for an improvement of one score for each of these traits is therefore somewhat arbitrary, since it has a threshold value that is difficult to determine.

Nonetheless, the input parameters that were used for demonstration purposes in the selection index calculations are presented in Table 7.3.

Table 7.3 (Co)variance ratios, phenotypic standard deviations (σ_p) and economic weights for ostrich slaughter and subjective skin traits

	Trait ^a				
	LW	CSS	NSZ	NS	HF
Phenotypic standard deviation (σ_p)	13.52	10.55	1.05	1.14	1.54
Economic weight ^b	ZAR 12/kg	ZAR 11/dm ²	ZAR 30/1 score	ZAR 30/1 score	ZAR -13/1 score
Heritabilities (in bold on the diagonal), genetic correlations (above) and phenotypic correlations (below the diagonal)					
LW	0.48	0.94	0.37	0.16	-0.17
CSS	0.79	0.51	0.51	0.39	-0.26
NSZ	0.40	0.49	0.34	0.72	0.08
NS	0.16	0.23	0.51	0.37	0.01
HF	0.03	-0.00	0.11	0.05	0.50

^a LW: Live weight; CSS: crust skin size; NSZ: nodule size score; NS: nodule shape score; HF: hair follicle score

^b In South African Rand (ZAR) per unit

The following sources of information were assumed for the respective traits:

- Pre-slaughter live weight – the individual to be selected, records of its sire and dam, as well as that of 10 full sibs;
- Crust skin size – records of 10 full sibs;
- Nodule size score – records of 10 full sibs;
- Nodule shape score – records of 10 full sibs;
- Hair follicle score – records of 10 full sibs.

Three scenarios were considered, namely:

1. when all the information was utilised,
2. when only records from live animals were available (i.e. pre-slaughter live weight),
3. and when only the live weight of the animals to be selected was used (as would be available in commercial flocks without pedigree information).

The contribution of each trait to the total monetary gain was remarkably constant between scenarios, amounting to 53 - 55% for pre-slaughter live weight, 38 - 39% for crust skin size, 3 - 4% for nodule size score, 2 - 3% for nodule shape score and 1 - 2% for hair follicle score. It is noteworthy that the subjective scores did not contribute markedly to monetary gain. Even when the economic values thereof was increased three times (to represent a more robust effect of scoring on grading), the contribution of these traits to the total monetary gain was only 12, 11 and 5%, respectively.

Responses were predicted at a selection intensity of 1, namely when ~38% of the animals are selected. As selection in ostriches can be quite intense owing to their relative large progeny sizes, it was assumed that 10% of animals from both genders were selected (assuming that all selected progeny would go into a pair-mating breeding system). The responses were also expressed per year, by dividing by an average generation interval of 7.72 years, as reported by Fair *et al.* (2012). The outcome from these calculations in terms of the genetic gain in ZAR terms per year is provided in Table 7.4.

Table 7.4 Output from MTINDEX depicting the genetic gain in monetary terms for each trait under three scenarios: Scenario 1 – live weight records for the animal, sire and dam, as well as 10 full sibs, as well as slaughter trait information for 10 full sibs; Scenario 2 – only live weight information for the animal, sire and dam, as well as 10 full sibs (no slaughter information); Scenario 3 – only live weight information for the animal to be selected

Trait	Monetary gain per year (ZAR)		
	Scenario 1	Scenario 2	Scenario 3
Pre-slaughter live weight	19.53	19.99	17.67
Crust skin size	14.38	13.83	12.22
Nodule size score	1.53	1.21	1.07
Nodule shape score	1.15	0.59	0.52
Hair follicle score	0.62	0.43	0.38
Total response	37.20	36.05	31.86

It is clear that the impact of not including the slaughter traits in the index in scenario 2 only had a marginal effect on trait monetary gains per year in terms of ZAR. Total slaughter income is approximately ZAR 2000, so a difference of ZAR 1.15 can be considered marginal. Even the exclusion of all information from relatives and only retaining individual pre-slaughter live weights still resulted in fairly high levels of progress in monetary terms per year. It thus seems feasible to make worthwhile monetary progress in all slaughter traits, even when minimal information can be obtained in the event of not having access to information on the pedigree and production levels of related animals.

The information supplied above make it evident that monetary genetic gains in slaughter bird production should be easy to achieve throughout the industry, at all levels of recording. This will be good news for a beleaguered industry that is still reeling from the impact of the recent outbreak of avian influenza.

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CHAPTER 8

Conclusions and recommendations

It was established in Chapter 2 that ostrich live weight is variable and heritable, and should thus respond to selection. The issue of using early body weight as an early predictor of slaughter weight was raised. It was contended that selection for an increase in bodyweight at any particular age (with the possible exception of 1 month of age) is likely to result in an increase in bodyweight at all ages. Genetic correlations among weights recorded from four months of age onwards were high throughout, in some cases not different from unity, indicating that selection from four months of age onwards will lead to substantive correlated responses in weights at later ages. It would therefore be possible to increase live weight at slaughter age through indirect genetic selection based on earlier weights as indicator traits. This could also assist in identifying replacement breeding stock at an early age to separate them from the commercial slaughter birds.

The efficacy of indirect selection at earlier ages for live weight at 13 months can be derived by using the following formula provided by Falconer (1989):

$$\frac{CR}{D} = r_g \cdot \frac{\sqrt{h_c^2}}{\sqrt{h_D^2}} \quad \text{with:}$$

$\frac{CR}{D}$ = the ratio depicting the efficacy of indirect selection using a correlated trait relative to direct selection for the trait of interest (in this case live weight at 13 months)

r_g = the genetic correlation between the traits

$\sqrt{h_c^2}$ = the square root of the heritability of the correlated trait

$\sqrt{h_D^2}$ = the square root of the heritability of live weight at 13 months

It could be established that selection based on 1-month live weight as an indirect trait for live weight at 13 months of age would only result in 35% of the gain achievable by direct selection. Likewise, selection on 4-month live weight, 7-month live weight and 10-month live weight would result in respectively 60%, 77% and 96% of the genetic gains based on direct selection for live weight at 13 months of age. Selection on 10-month live weight would thus be almost just as efficient as direct selection, and have the added advantage that the number of potential replacement birds could be narrowed down during a period when feed costs are at its highest. Only birds with higher live weights could thus be retained to meet replacement needs. It thus seems reasonable to argue that preliminary selection on live weight to reduce the number of birds needed for replacement may be a viable practice to reduce feeding costs and also to market surplus birds before

they become less feed efficient. Replacement birds could be separated from slaughter birds at an earlier stage and fed with maintenance diets instead of the more expensive finisher diets used for slaughter production.

Genetic parameters involving quantitative slaughter traits in Chapters 3 and 5 indicated that all traits are heritable and variable and should respond to purposeful selection. The most important exception to this rule is the economically important trait of skin grading, which would need to be improved by managerial interventions and adapted husbandry practices.

It is furthermore evident from the study that the vast majority of quantitative meat and skin traits are favourably related to live weight (as a quantitative slaughter trait measurable on the live animal). Traits that are unrelated to live weight can be improved largely independent from weight or size. Neckline traits seem to fall in the latter category, and may be improved independently from live weight and crust skin size.

When the traits associated with crown size were considered, it seemed that the increase of crown size independently from the size of the animal would be challenging. The major disadvantage of both neckline traits and crown traits is that there is presently no clear indication of potential economic gains associated with these traits as the present payment scheme functions solely on crust skin size, skin grading and nodule development.

Slaughter production for meat is mostly quantitative in the ostrich industry, as there is no incentive for producers to produce meat with better quality at present, with prize per kilogram increasing as carcass weight increases. The only possible penalty producers could incur is when carcasses are partly or wholly downgraded because of disease or bruising. Yet it is notable that potentially important meat quality traits like ultimate pH and lightness do exhibit genetic variation, and would possibly respond to selection (Chapter 4). This was true even though the data set available for studying meat quality traits was less than optimal by own admission.

When the qualitative skin traits were considered in Chapter 6, the most striking observation was that the linear scores allocated to skins were all highly heritable and favourably correlated with live weight and crust skin size on the genetic level. This outcome assures that it should be relatively easy to construct a breeding strategy involving all these traits.

In stark contrast with qualitative meat traits where there does not appear to be monetary incentives for improvement, skin quality traits like nodule size and nodule shape as well as hair follicles do exert an important influence on skin grading (Engelbrecht *et al.*, 2009) and therefore has economic value. Skins are downgraded if nodule development, which is collectively determined by nodule size and nodule shape, is found to be unacceptable, with mostly small, poorly developed nodules. Skins are also downgraded for the excessive occurrence of hair follicles. All these components of skin quality can be improved genetically as

reported in Chapter 6. Purposeful genetic selection is thus highly likely to benefit aspects of skin grading and therefore the unit price of the product.

Lastly, it was evident that monetary genetic gains in slaughter bird production should be easy to achieve throughout the industry, at all levels of recording, by making use of a simple selection index as described in Chapter 7.

Recommendations pertaining to future research

The study revealed several aspects that need further consideration in future research. The following issues became evident during the study:

It is noteworthy that the live weight of ostriches has featured strongly throughout this study, and that it is instrumental to almost all outcomes reported. Yet there is limited information on feed efficiency, and absolutely no information on the genetic basis of efficiency in this species. Research to fill this gap is also urgently needed. Given the dominant role that live weight (or size) played in the deliberations so far it would be of future interest to know if the continuous improvement of live weight in ostriches is advisable from an efficiency perspective.

Weights recorded at specific ages were evaluated as separate traits, according to general practice. However, this approach has limitations as to how many traits can be analysed, with consequent data loss as measurements outside of the established age ranges are eliminated (Sanchez *et al.*, 2008). An alternative option would be to model the pattern of animal growth over time with longitudinal models, which have the advantage that weight can be measured at any point along a trajectory, allowing the use of all available records (Van der Werf, 2005). Random regression models have been extensively applied in genetic analysis of longitudinal data (Miszta, 2006) to successfully model the pattern of animal growth over time; enabling the study of changes in genetic variability with time (Schaeffer, 2004). It has statistical advantages as well, needing fewer parameters to describe the same data as a multi-trait model (Huisman *et al.*, 2002) and requiring less memory and time than some multi-trait analyses (Nobre *et al.*, 2002). The use of random regression models to estimate genetic parameters for growth, as first proposed by Kirkpatrick *et al.* (1990), have consequently replaced nearly all analyses of growth traits (Schaeffer & Jamrozik, 2008) and has been used successfully to estimate genetic parameters for growth in various species (Schaeffer & Jamrozik, 2008), including swine (Huisman *et al.*, 2002) and beef cattle (Meyer, 2004; Nephawe, 2004).

Random regression models are deemed appropriate when there are varying numbers of measurements and when all animals have multiple measurements (Schaeffer, 2004) – as was the case with ostrich growth data. The accuracy of the genetic evaluation for ostrich growth can potentially be improved by replacing a multi-trait model (as used in Chapter 2) with a random regression model, as illustrated by Meyer (2004) for beef

cattle data. The random regression approach should therefore be considered to investigate trends for ostrich growth further and to estimate genetic variability over time, making use of all the available data.

In Chapter 3, it is stated that fat from the ostrich slaughter industry are treated as a waste-product at present. Yet, when the medicinal value of oil derived from emu fat is considered (Sales, 2007; Bennett *et al.*, 2008), it is clear that there is room for developing ostrich fat into an additional source of income for ostrich farmers. The genetic information supplied in Chapter 3 indicates that it would be relatively straightforward to incorporate fat yield as part of an economic selection index. Attention should be given to the possibility of further diversification in terms of products in the industry.

Chapter 4 reports on qualitative meat traits, based on limited records. Although the results that were found are highly encouraging, it should be a high priority to expand the data base so that genetic parameters can be based on more acceptable numbers of records. The technology to assess meat quality for a number of traits is available in other species (Ripoll *et al.*, 2008; Prieto *et al.*, 2009; Engel *et al.*, 2012), and it should also be applied to ostriches to assist in collection of sufficient data for parameter estimation. It is generally accepted that tenderness is the most important meat quality trait. Tenderness was shown to be one of the best-predicted variables with near-infrared reflectance spectroscopy (Ripoll *et al.*, 2008). A conscious effort should be made to measure tenderness in sufficient numbers to validate the estimation of genetic variation for this trait in ostriches, as well as genetic correlations with other traits. This intervention is even more important if it is considered that ostrich meat is being marketed as a high-value lean product, with a strong focus on meat quality (Balog & Almeida Paz, 2007). Currently incentives for the production of high quality ostrich meat is lacking however.

It is clear from Chapters 5 and 6 that obtaining accurate data on skin traits are problematic and that evaluation of skins rely to a large extent on indirect or subjective measures of quality. The lack of objective evaluation methods for accurate determination of skin quality hampers progress and need to be urgently addressed. As skin quality can only be assessed after slaughter, an important field of study would be to investigate and identify methods of accurately determining skin quality on the live bird. The use of imaging technologies for the detection of defects and accurate assessment of skin quality after slaughter should also be investigated and developed. Accurate assessment of quality and early detection of defects will promote the use of appropriate processing techniques that can potentially result in improved utilisation of skins, while it will aid in establishing accurate parameters for skin traits.

The presence of a dam permanent environmental variance component amounting to approximately 5-10% at relatively late ages was, to a large extent, a feature of the results of almost all chapters. These permanent environmental variances mostly seemed to be accounted for by information contained in other traits when combined in multi-trait analyses. It may be speculated that these effects are associated with the pair-mating system employed in the resource population, as there is bound to be high sampling correlations between sire and dam effects. It will be most informative to experiment with data obtained from alternative mating systems to be able to control the partitioning of direct and maternal variances better. There is the possibility

that artificial insemination may become a viable option in ostriches in future (Malecki *et al.*, 2008, Malecki & Rybnik-Trzaskowska, 2011) that will have a marked beneficial effect upon data structure in this species (Cloete *et al.*, 2008). It should be seen as a priority to analyse data derived from alternative mating structures as soon as such data become available.

The combination of slaughter traits in the index reported in Chapter 7 has the potential to be refined appreciably, using the software of Van der Werf (2008). Further traits to consider may involve meat traits, as well as skin traits that do not have direct economic values as of yet. The outcomes of selection based on the present knowledge on these traits also need to be ascertained. Apart from that, it would also be feasible to include the concept of early selection as concluded upon at the beginning of this chapter in a more structured way by including the early weight traits in an index.

Although a selection index for slaughter bird production appears to be relatively straightforward when the slaughter traits of present economic importance is considered, it does not address ostrich farming as a whole. Other important production functions like feather production, feather quality, reproduction (incorporating the production of eggs and chicks, as well all components of reproductive and hatching failure) and chick survival have not been taken into account. Kluyts *et al.* (2007) warned that it is important that all traits of economic importance must be considered in a multi-trait BLUP (Best Linear Unbiased Prediction) model to allow the construction of an optimal selection index. A comprehensive selection index, based on all the relevant traits, should therefore ultimately be constructed for the industry; keeping in mind that considering too many traits during selection can seriously hamper the progress in economically important traits (Olivier, 1991).

An index constructed from data on a herd or flock in one locality, as was the case in this study, may not be widely applicable (Hazel, 1943) and obtaining information from other flocks and locations would be preferable. This may however not be feasible in the ostrich industry where the availability of other pedigreed populations with suitable data is very limited (Cloete *et al.*, 2008). The industry is also very localized, with more than 70% of ostriches globally found in South Africa (Anon., 2012) and about 50 % of the total number of ostriches in South Africa found in the Oudtshoorn district (Mugido *et al.*, 2012).

This study mostly dealt with additive genetic principles, and has shown that additive gains are indeed highly feasible for the vast majority of traits studied. However, the ostrich industry could also potentially benefit from commercial heterosis. While crossbreeding options have been considered for meat traits (Hoffman *et al.*, 2007; Davids *et al.*, 2010), no such work has been done for skin traits so far. Moreover, sexual dimorphism appears to be largely absent in ostriches. However, advances following from feeder-breeder dimorphism may still add to commercial efficiency provided that different ostrich strains are dimorphic for size (Jarvis, 1998, Engelbrecht *et al.*, 2008; Davids *et al.*, 2010). Engelbrecht *et al.* (2008) indicated that the introduction of Zimbabwean Blue (*Struthio camelus australis*) ostriches into commercial ostrich flocks can have benefits with regard to direct heterosis for growth. When considering the results of this study it is plausible that skin size would also benefit as a result. The effect of crossbreeding on skin quality is largely

unknown, however, and needs to be determined. It is well known that the feather quality of Zimbabwean Blue ostriches is far inferior to that of South African Black ostriches, a strain specifically developed for superior feather quality. Due to the relationship between feather quality and leather quality, it will be eminent to investigate the effect of crossbreeding on both feather and leather quality. As crossbreeding becomes more important in the industry, more research on these topics will be critical.

Furthermore, value-adding has become more important in all industries. Aspects of value adding and processing of ratite meat have been investigated as reviewed by Hoffman (2008). There still remains scope to do more research on this topic, however, particularly involving secondary products like fat.

Finally, this research has shown that there is substantial scope for improving quantitative and qualitative ostrich slaughter traits through genetic selection. While industry can immediately benefit from some of the findings that were reported here, there are several aspects that need further consideration. The possibilities of improving the production environment as well as the challenges to establish breeding plans for genetic improvement of the most important economic traits of slaughter ostriches were shown.

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