THE GENETIC AND ENVIRONMENTAL MODELLING OF PRODUCTION AND REPRODUCTION IN OSTRICH FEMALES WITHIN AND ACROSS BREEDING SEASONS

by

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"I Michael Denis Fair declare that the thesis hereby submitted by me for the PhD degree at the University of the Free State is my own independent work and has not previously been submitted by me at another university/faculty. I furthermore cede copyright of the thesis in favour of the University of the Free State."

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M.D. Fair

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Acknowledgements

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Publications in peer reviewed journals:

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Abstract

Pedigree and performance data of a well-documented ostrich breeding resource flock was used to (1) investigate the flock structure, (2) estimate variance and (co)variance components for egg and day-old chick weight (individual traits), (3) estimate genetic and environmental parameters for egg and chick production, mean egg and day-old chick weights and hatchability *within* breeding seasons (hen traits) and (4) investigate early identification of superior animals using random regression models for repeated measures (longitudinal) data over years.

The average level of pedigree completeness of 40 074 birds of a pair-breeding ostrich flock maintained from 1978 to 2005 at the Oudtshoorn Research Farm, South Africa was high (99.3%) in the first generation and the average level of inbreeding (F) was low at 0.51%. The estimated measures of variability were: effective genome equivalents = 47.3, effective number of founders = 59 and the effective number of ancestors = 58. The numbers of ancestors responsible for 100%, 50% and 20% of the variation in the reference population (birds with both parents known), were equal to 254, 21 and 6 respectively. The generation interval in years calculated as the average age of parents when their offspring which were kept for reproduction were born, amounted to 7.72 ± 4.79 years. The linear regressions of rate of inbreeding on year of hatch for the two distinct periods, 1995-2002 and 2003-2005, were 0.08% and -0.07 % per year respectively. The estimate of effective population size (N_e) computed via the increase in the individual rate of inbreeding was 112.7 animals. The results of this study indicated that the population under study was at an acceptable level of genetic variability.

Pedigree and performance data for 71 147 individual egg records collected between 1991 to 2005 were used to estimate genetic parameters for egg weight (EWT), live day-old chick weight (CWT) and hatchability (H). Heritability estimates (±SE) were 0.12 ± 0.02, 0.14 ± 0.04 and 0.09 ± 0.04 for EWT, CWT and H. Corresponding estimates for maternal genetic effects were 0.27 ± 0.08, 0.38 ± 0.08 and 0.13 ± 0.02. The effects of common environment, permanent environment and breeding paddock were significant but relatively low for all traits. Egg weight and CWT were highly correlated at all levels, while H was mostly independent of the

weight traits. These results indicated that genetic improvement in these traits would be feasible.

Data involving monthly records of egg production (EP), chick production (CP), hatchability (H), mean egg weight (MEW) and mean day-old chick weight (MCW) were analysed as hen traits. Heritability estimates amounted to 0.04 ± 0.02 for EP, 0.05 ± 0.03 for CP, 0.44 ± 0.04 for MEW, 0.02 ± 0.02 for H and 0.67 ± 0.02 for MCW. Permanent environmental effects as a ratio of phenotypic variance (c^2_{pe}) ranged from 0.08 ± 0.03 to 0.11 ± 0.02 for the first four traits (MCW did not exhibit a significant c^2_{pe} effect). Monthly EP and CP were highly correlated at all levels, ranging from 0.74 for the temporary environmental correlation to unity for the genetic correlation. Hatchability was highly correlated with EP and CP at the genetic level (>0.94). Genetic correlations of EP and CP with MEW and MCW were variable and in some cases antagonistic. Genetic correlations of H with MEW and MCW were positive (0.52 and 0.47, respectively). Results indicate that selection for improved reproduction (reproductive output and product quality traits) is feasible. Selection for production is unlikely to be complicated by unfavourable correlations with H, MEW and MCW.

Hen traits defined above were further analysed in single-trait mixed models with a random regression fitted as an intercept for the direct animal (a) and a quadratic polynomial with intercept for the permanent environmental (p) effect peculiar to each hen. Heritability (h^2) estimates were moderate and remained relatively constant for EP and CP ranging from 0.13-0.14 and 0.07-0.08 respectively for 3- to 10-year old hens. Quality traits MEW and MCW had moderately high h^2 estimates ranging from 0.49-0.61 and 0.37-0.45 respectively. Hatchability had h^2 estimates ranging from 0.11-0.13 for the 10 hen-ages. Permanent environment variance ratio for EP, CP, MEW, MCW and H ranges were 0.28-0.42, 0.29-0.41, 0.17-0.33, 0.21-0.35 and 0.14-0.24 respectively. Selection of superior hens from three years onwards seems possible. Hens older than eleven years should be replaced with younger, genetically superior hens which would reduce the generation interval and improve EP and CP genetically, without adversely affecting MEW, MCW and H.

Opsomming

Note to the reader: This section is written in Afrikaans and is a translation of the preceding abstract.

Stamboom-en prestasie-data van 'n goed gedokumenteerde volstruis telinghulpbron-kudde is gebruik om (1) ondersoek intestel na die kuddestruktuur, (2) beraamde variansie en (ko)variansie komponente vir eier- en dag-oud kuiken-gewigte (eienskappe van die individu), (3) genetiese- en omgewingparameters te beraam vir eierproduksie, kuikenproduksie sowel as vir gemiddelde eier- en dag-oudkuikengewig en uitbroeibaarheid binne teelseisoene (wyfie-eienskappe) en (4) die vroeë identifisering van diere met hoë genetiese meriete deur die gebruik/ ondersoek van toevalsregressiemodelle vir herhaalde metings van rekords oor jare.

Die gemiddelde vlak van die stamboomvolledigheid van 40 074 eiers van 'n afgepaarde volstruisbroeitrop, vanaf 1978 tot 2005 op die Oudtshoorn Navorsingsplaas, Suid-Afrika was hoog (99.3%) in die eerste generasie en die gemiddelde vlak van inteling (F) was laag op 0.51%. Die beraamde maatstawwe van variasie was: effektiewe genoom ekwivalente = 47.3, effektiewe aantal stigters = 59 en die effektiewe aantal voorvaders = 58. Die getalle voorvaders verantwoordelik vir 100%, 50% en 20% van die variasie in die verwysingspopulasie (voëls met beide ouers bekend), was onderskeidelik 254, 21 en 6. Die generasie-interval, aangedui in jare, bereken as die gemiddelde ouderdom van die ouers wanneer hulle nageslag wat vir reproduksie doeleindes geselekteer is, gebore word, het 7.70 ± 4.87 jaar beloop. Die lineêre regressies van die tempo van inteling op jaar van uitbroei vir die twee afsonderlike periodes, 1995 - 2002 en 2003-2005, was onderskeidelik 0.08% en -0.07% per jaar. Die beraming van die effektiewe bevolkingsgrootte (N_e) bereken deur middel van die toename in die individuele koers van inteling was 112.7 diere. Die resultate van hierdie studie het aangedui dat die populasie tans aanvaarbare vlakke van genetiese variansie handaaf.

Stamboom- en prestasie-data van 71 147 individuele eierrekords tussen 1991 tot 2005 ingesamel, is gebruik om genetiese parameters te beraam vir eiergewig (EWT), dag-oudkuiken-gewig (CWT) en uitbroeibaarheid (H).

Oorerflikheidsberamings (± SE) was onderskeidelik 0.12 ± 0.02, 0.14 ± 0.04 en 0.09 ± 0.04 vir EWT, CWT en H. Ooreenstemmende beramings vir die maternale genetiese effekte was onderskeidelik 0.27 ± 0.08, 0.38 ± 0.08 en 0.13 ± 0.02. Die toevallige effekte van die wyfie se algemene-, en permanente-omgewing sowel as die broeikamp was statisties betekenisvol maar relatief laag vir al die eienskappe. EWT en CWT was hoogs gekorreleer by alle vlakke, terwyl H meestal onafhanklik van die gewig eienskappe was. Hierdie resultate dui daarop aan dat die genetiese verbetering wan die eienskappe haalbaar sou wees.

Data met betrekking tot maandelikse rekords van eierproduksie (EP), kuikenproduksie (CP) en uitbroeibaarheid (H), gemiddelde eiergewig (MEW) en gemiddelde dag-oudkuiken-gewig (MCW) is ontleed as eienskappe van die hen. Oorerflikheidsberamings was 0.04 ± 0.02 vir EP, 0.05 ± 0.03 vir CP, 0.44 ± 0.04 vir MEW, 0.02 ± 0.02 vir H en 0.67 ± 0.02 vir MCW. Permanente omgewing (c^2_{pe}) as 'n proporsie van fenotipiese variansie het gewissel tussen 0.08 ± 0.03 en 0.11 ± 0.02 vir die eerste vier eienskappe (MCW het nie 'n betekenisvolle c^2_{pe} effek getoon nie). Maandelikse EP en CP was hoog gekorreleerd op alle vlakke, en was tussen 0.74 vir die tydelike omgewingskorrelasie en 1.00 vir die genetiese korrelasie. H was hoogs gekorreleerd met EP sowel as CP op die genetiese vlak (> 0.94). Die genetiese korrelasies van EP en CP met MEW en MCW was wisselend in grootte en soms antagonisties. Die genetiese korrelasies van H met MEW en MCW was positief (0.52 en 0.47). Die resultate dui daarop dat seleksie vir verbetering van reproduksie (reproduktiewe uitset en kwaliteit van die produk eienskappe) haalbaar is. Seleksie vir produksie hoort nie gekortwiek te word deur ongunstige korrelasies tussen H, MEW en MCW.

Heneienskappe hierbo beskryf is ook as enkel-eienskap gemengde modelle ontleed, met 'n toevalsregressie gepas as 'n afsnit vir die dier (a) en 'n kwadratiese polinoom met 'n afsnit op die y-as vir die permanente omgewingseffek wat eie is aan elke wyfie. Oorerflikheidsberamings (h^2) was matig en relatief konstant vir die EP en CP wat gevarieer het tussen 0.13-0.14 en 0.07-0.08 onderskeidelik vir 3- tot 10-jaar-oue wyfies. Die gehalte-eienskappe MEW en MCW het redelik hoë h^2 beraamings van tussen 0.49-0.61 en 0.37-0.45 getoon. H se h^2 het tuseen 0.11 en 0.13 vir die 10 hen-ouderdomsgroepe gevarieer. Die permanente omgewings variansieverhoudings vir EP, CP, MEW, MCW en H het onderskeidelik tussen 0.28-0.42, 0.29-0.41, 0.17-0.33, 0.21-0.35 en 0.14-0.24 gevarieer. Seleksie van drie-jaar-oue henne blyk

uitvoerbaar te wees. Voëls ouer as 11 jaar hoort met jonger geneties verbeterde wyfies vervang te word. Die generasie interval sou daardeur verlaag word, terwyl EP en CP additiewe genetiese vordering kan toon, sonder noemenswaardige nadelige invloede op MEW, MCW en H.

1

GENERAL INTRODUCTION

1.1 Introduction

Ostriches (*Struthio Camelus*) form part of the group of birds known as ratites (flightless birds) and have been on the earth for the last ± 120 million years according to general consensus among scientists. References to ostriches date back to the Bible and ostrich figures feature in hieroglyphics found in Egypt's pyramids and historical places (Burr, 1955).

The farming of ostrich on a commercial basis started in South Africa in the mid 1800's between 1838 and 1866 (Mosenthal & Harting, 1897; Gobel, 1994). Initially ostriches were commercially farmed for their feathers for use mainly in the fashion industry. World demand, largely from Europe, for feathers reached its peak in 1913 causing South African ostrich feathers to be the fourth largest national export product trumped only by gold, diamonds and wool. It was estimated that there were as many as one million birds in South Africa at that time (Gertenbach, 2006). World War I caused the feather market to collapse due to suppressed demand. By 1930 the number of captive ostriches for commercial production dropped to as low as 23 000 birds (Smit, 1963; South African Ostrich Business Chamber, 2004).

The ostrich industry in South Africa started to recover only after World War II in the early 1950's (Smith *et al*., 1995) due to demand for ostrich skins (leather), with their unique quill pattern and superior strength, and later, from the 1980's, for a healthy, low in cholesterol, alternative source of red meat. Brand & Jordaan (2011) reported that South Africa produced 70% of the ostrich meat, leather and feathers on the world market. World production of ostriches for slaughter in 2004/05 were close to 420 000 of which 291 000 birds were slaughtered in South Africa. Local slaughter production thus contributed 69% to the total number of birds slaughtered worldwide, indicating the importance of the ostrich industry in South Africa.

The modernising of the ostrich industry in terms of breeding practices requires careful consideration of the requirements of the consumer and downstream processing industries in terms of product quality. Genetic knowledge of traits of economic importance is necessary when planning a selection programme to meet these needs.

Modern breeding techniques and tools are available to the animal breeder and are well developed in the livestock industries. These techniques rely on sound records of ancestry (pedigree records) linked to performance data of relatives and progeny, which on the whole are lacking in the commercial ostrich industry.

Pedigree and performance information of commercial ostriches are not available in South Africa. In contrast, the Oudtshoorn Research Farm has a carefully defined set of records of performance and pedigree data of a well-maintained and -managed ostrich flock, giving researchers an opportunity to derive genetic parameters that are helpful when designing modern breeding programmes. The birds are managed as a pair breeding flock. Males and females are kept together as pairs in separate breeding paddocks allowing the recording of ancestry pertaining to eggs produced. These records present an opportunity to examine the pedigree structure, level of inbreeding, generation interval, effective population size and founder contributions of a well-recorded flock. Knowledge of these parameters could assist the industry when formulating breeding programmes and form a baseline for the particular flock for future reference and control.

Increasing farm profitability is an ongoing crusade of most role players in the agricultural sector. One method of achieving this goal is through higher income and reduced costs. This can be done by genetically improving, modifying or optimizing flocks, allowing the change in the genotypic makeup of the animals to inherently cope with and meet the demands of local and international consumers. Selecting superior animals with optimum performance levels according to the demands (of consumer and environment) would improve the mean flock production levels and ultimately profitability. Identification of relevant economic traits of production and reproduction is thus vital when designing a breeding programme. The traits should be economically important (both for the producer and consumer) and accurately measurable. Measurability of the trait allows for accurate determination of the current state of the flock to use as a benchmark and then later the means to evaluate progress made in the improvement or maintenance (at an optimum level) of the trait in question. The income from meat and leather in the ostrich industry each contribute equally to the

income of farmers and accounts for roughly 90% of the total income, while income from the feathers account for the remaining 10% (Hoffman, 2005).

Cloete *et al*. (2002) suggested that, given the high percentage of income derived from skins and meat, a large number of high quality chicks surviving to slaughter should play the most important role in setting selection objectives. Some South African ostrich breeders obtain income exclusively from the sale of day-old chicks. Greater numbers of viable, good quality chicks produced per breeder bird would thus directly influence the income of this sector of the industry. An increased number of fertile eggs that hatch and survive would thus be equally important. Analyses to determine genetic parameters of these traits are required to determine the amount of variability and whether correlated responses exist. Unfavourable correlations could be counterproductive when more than one trait is considered during selection. An increased number of eggs and hatched chicks would also increase the "pool" of genetic material available for selection.

Measured phenotypic variance is unfortunately not exclusively due to genotypic differences but also the result of non-genetic and environmental factors. Identification and estimation of these factors help quantify contributing influences responsible for the performance of the birds measured. Knowledge of these factors can be put to use mainly via adapting and changing management practices to enhance production and reproduction. Non genetic effects typically found in animal production such as age of parents, gender of animal, contemporary groups, year, season, parity, sequence and litter to mention a few need to be estimated and assessed for inclusion in models used to estimate breeding values (EBV's). Inclusion of measures of environmental variation in the model used for analysis ensures more accurate additive genetic variances and EBV's.

Selection for increased production levels of number of egg and chicks need to be balanced so as not to compromise the associated quality traits of mean egg and day-old chick weight as well as hatchability. Prolonged selection pressure for increased production only, could lead to lower mean egg weights and compromise chick vitality and hatchability.

The potential for genetic improvement is largely dependent on the heritability of the trait and its genetic relationship with other traits of economic importance upon which selection pressure may be applied. Information on genetic parameters is

essential for planning efficient breeding programmes, and for predicting response to selection.

Due to the low heritability of fitness traits such as hatchability the most promising route for optimization of an enterprise will be via management practices. However, low heritability does not exclude improvement by selection; it only takes a long time to see measurable results. Moreover, reproduction traits often exhibit higher levels of phenotypic variation than other production traits, which would facilitate genetic progress in a focused selection strategy. Literature estimates of heritability for hatchability of fertile eggs of chickens ranges from 0.02 to 0.24 (Förster, 1993; Beaumont *et al*., 1997; Szwaczkowski *et al*., 2000; Sapp *et al*., 2004; Bennewitz *et al*., 2007; Rozempolska-Rucinska *et al*., 2009; Sharifi *et al*., 2010; Wolc *et al*., 2010). These estimates from the literature are normally difficult to compare, due to differences in trait definitions, collection and structure of the data and statistical models used in their analyses. According to Sapp *et al*. (2004) and Swalve (1995) the use of a cumulative model may overestimate the heritability. By averaging fertility over several weeks, either by pooling all weeks or by calculating average fertility per week, higher heritability and accuracy of selection can be obtained (Wolc *et al*., 2009).

According to Wolc *et al.* (2010) hatchability in chickens is almost exclusively a trait of the hen when considered independent of fertility. Careful consideration should therefore be given to the dam and maternal grand dam genetic pathways when trying to select males for higher hatchability of fertile eggs.

According to Bunter & Cloete (2004) several factors have hindered the estimation of accurate genetic parameters for performance traits in ostriches. Parentage of eggs and chicks is normally unknown due to the sharing of communal nests by colony mated ostriches. These data are unusable for the estimation of genetic parameters unless pedigrees can be established by more sophisticated alternatives including DNA parentage determination. No commercial DNA service for parentage in ostriches is in operation at present, and a lack of long-term stability in the industry probably constrains developments in this regard (Cloete *et al.,* 2002).

Bunter & Cloete (2004) furthermore referred to the existence of evidence suggesting that ostriches are induced breeders, are territorial, and create pair bonds with their mates. While traditional management strategies for pair-breeding flocks (repeat mating of the same pair in the same breeding paddock, year after year) allow

for such behavior, this also compromises data structure for estimation purposes, although pedigree is known. Lastly, ostrich flocks typically have small flock sizes with a relatively slow turnover, leading to comparatively few replacements being selected annually (Cloete *et al.,* 1998) and reduce both the number of parents with progeny as well as generations with records represented.

Early identification and selection of genetically superior birds, that maintain high production over their lifetime, could mean the shortening of the generation interval and progress towards increased production levels. At this stage, it is unknown whether the heritability of repeated performance traits of ostrich females across subsequent production seasons changes with age.

Repeated performance traits of ostrich females across subsequent production seasons changes with age. Information on these traits can be defined as "longitudinal" data (Meyer & Hill, 1997). Several different methods have been implemented by research groups to properly model these data types in especially pig, beef and dairy traits. In a recent paper Speidel *et al*. (2010) reviewed the development and assumptions of the different methods used to analyse longitudinal data. Analysis of the changes over time can be undertaken using repeatability (Henderson, 1984), multiple trait or the more contemporary (and perhaps more appropriate) random regression models (RRM) (Mrode, 2005). Random regression (Meyer, 1998) allows for the calculation of (co) variances at every age.

Perhaps the simplest method of analysis of longitudinal data is the repeatability model. The philosophy behind this model is to treat each observation as a repeated record of the same trait on the same individual. This model has been implemented in the past for several traits in several livestock species (Speidel *et al*., 2010). It has also been the model of choice in the previous studies on ostriches (Cloete et al., 2004; 2006; 2008a).

Multiple-trait genetic evaluation, as introduced by Henderson & Quaas (1976), predicts genetic values for more than one trait through the incorporation of the genetic and residual (co)variances between the traits (Mrode, 2005). This property can be extended to the analysis of longitudinal data where different traits of an individual animal are treated as separate but genetically correlated traits. It is under this assumption that the majority of current national genetic evaluation systems in different species are performed.

According to Speidel *et al*. (2010) multiple-trait models have two inherent problems when analyzing longitudinal data. Firstly the large number of data points can lead to equation systems that have very high dimension and computational requirements. Secondly they have the potential for high correlations between successive measurements which is undesirable for two main reasons. If two traits predict the same information, it is senseless to include both of the traits in the model. Furthermore, the correlation between the two traits has the effect of reducing the power of the tests of significance (Foster *et al*., 2006). One technique how to specifically handle these elevated correlations is referred to as autoregression or autocorrelation, which has been documented in the literature numerous times (Harville, 1979; Kachman & Everett, 1993; Carvalheira *et al*., 1998)

Random regression models (RRM) to analyse longitudinal or repeated measures data have become common practice amongst animal breeders (Schaeffer, 2004; Tier & Meyer, 2004; Buxadera & da Mota, 2008; Wolc *et al.,* 2009). RRM are similar to multiple-trait models in that a number of correlated additive genetic effects, namely regression coefficients, are estimated for each individual. Estimates of genetic RR coefficients provide a complete trajectory of genetic merit. Estimated breeding values for any point on the longitudinal scale can be obtained by evaluating the regression equations at that point (Tier & Meyer, 2004). RRM results can thus be most useful to determine the point on the longitudinal trajectory when heritability peaks.

Areas of animal breeding that have already utilized RRM include conformation traits, body condition scores, feed intake, and heart girth measures in dairy cattle; weights and back fat thickness in swine and beef cattle; fork length and weights in rainbow trout; and litter size in swine. The first results using RRM models, regarding horse racing, specifically adapted to variation in horse age, was presented by Bugislaus *et al*. (2006), Other potential applications include wool yield in sheep; sperm production and quality in male reproduction of any species; lifetime milk production in dairy cattle; G x E interactions; survival analyses and female reproduction. RRM have also been used in human health studies and could be used in many biological situations (Scheaffer, 2004). The first estimates of variance components for test-day milk yields obtained by RRM were published by Jamrozik & Schaeffer (1997). Several reviews on the use of RRM for the analysis of test-day records of dairy cattle have been given (Swalve, 1998; 2000; Jensen, 2001; Dzomba

et al., 2010) Random regression has also been used to study egg production throughout a laying cycle in both broilers and turkeys (Anang *et al.,* 2002; Kranis *et al.*, 2007). The influence of season on total egg production, fertility, and hatchability in a male and female line of turkeys were investigated where each month was modeled as an independent variable (Case *et al.*, 2011). One of the objectives of the current study was to explore the use of random regression models to model egg and chick production over years as an alternative to a multiple trait analyses in an ostrich population.

The alternative analysis to random regression models would be to use multi-trait models with each successive year's production performance being modelled as a different trait. Case *et al.* (2011) emphasized that there are both advantages and disadvantages when using results from multiple-trait and random regression models (RRM) in a breeding program.

- RRMs can be implemented to model changes in genetic merit over the year on a continuous time scale. These results may, however, not be as easily implemented into a breeding program.

- The multiple-trait model allows the inclusion of two seasonal traits, each of which can be assigned equal or different weighting factors. It would be more difficult, however, to determine the weighting of regression coefficients in breeding program design as more "traits" are involved.

- RRM results can, however, be used to aid in multiple-trait selection. Monthly heritability estimates can indicate the best month/age group within each season/year to evaluate genetic merit. Selection decisions based on months/production years with the highest heritability can increase the rate of genetic improvement provided that the genetic correlation of the trait in the selected month/age group with the other months/age groups is high. The RRM is therefore more useful for evaluating the longitudinal nature of traits whereas two-trait models can be more easily implemented into breeding programs (Case *et al.*, 2011).

However, the number of records available in the ostrich resource population studied is not yet sufficient to use this method. This study therefore focuses on

exploring the use of random regression models to model production over years as an alternative.

Artificial insemination (AI) could play a role in changing the pedigree and data structure in the ostrich industry (Cloete *et al*., 2002; Cloete *et al*., 2008b). Advances in semen collection (Rybnik *et al*., 2007), and the insemination of receptive females for the production of fertilised eggs (Malecki & Rybnik, 2008; Malecki *et al*., 2008) have recently been made. Improved data structure because of AI together with better breeding programmes is likely to enhance additive genetic gains. This may be achieved by shortening the generation interval, identifying and selecting genetically superior birds for economically important traits. Managerial practices may also be adapted according to identified non-genetic effects. In combination, these advances could benefit the ostrich industry along its path to breeding modernisation.

The aim of this study was therefore to provide the South African ostrich industry with knowledge of flock structure, as well as genetic and environmental parameters influencing production and reproduction of ostrich females within and across breeding seasons. This knowledge could then be used when formulating modern breeding plans for implementation by the South African ostrich industry. This was achieved by:

(i)   Investigation of the available pedigree structure, inbreeding levels, generation interval, effective population size and founder contributions of a well-documented ostrich breeding resource flock,

(ii)   Estimation of variance and (co)variance components needed for genetic evaluation and quantify non-genetic effects affecting performance modelled with individual eggs/chicks as individuals,

(iii)   Estimation of genetic and environmental parameters for egg and chick production (quantity), mean egg and day-old chick weights and hatchability (quality) *within* breeding seasons and

(iv)   Investigation of the early identification of superior animals that maintain high production over their lifetime. This section focused on the viability of selection for increased total egg and chick production and the calculation of genetic and non-genetic parameters of these traits as well as exploring the use of random regression models for repeated measures (longitudinal) data over years.

The thesis is structured in the following way:

After a general introduction and aim statement in Chapter 1, an analysis of the pedigree structure of the Oudtshoorn Research Farm ostrich resource flock studied was conducted and presented in Chapter 2, using the ENDOG programme (version 4.8) (Gutiérrez & Goyache, 2005) to generate pedigree information of inbreeding levels, generation interval, effective population size and founder contributions. Chapter 3 estimated variance and (co)variance components for egg weight, chick weight and hatchability, all modelled as traits of the egg, while also modelling non-genetic effects in single-trait and two-trait animal models to derive genetic correlations and heritability estimates. Chapter 4 then further explores parameter estimates for reproductive output and production quality traits of ostrich females within breeding seasons, considered as traits of the hen. Chapter 5 explores the use of random regression models to model repeated measures (longitudinal) data over years, to establish the feasibility of early identification of superior birds for selection. Chapter 6 provides the general conclusions of the study and recommendations for the ostrich industry.

2

PEDIGREE ANALYSIS

2.1 Introduction

Domestic animal diversity is an integral part of global biodiversity, which requires sound management for sustainable use and future availability (FAO, 1992). The effective population size computed from the rate of inbreeding of a population is a measure of the genetic diversity and drift and is used for characterising the risk of extinction of animal populations and genetic variability available for future selection (Wright, 1969; Duchev *et al.*, 2006). The founder effect is a measure of the loss in genetic diversity caused through the formation of small groups of individuals which may remain isolated in a population. The founder effect contributes to genetic drift, which can play an important role in determining the genetic makeup of subsequent generations.

Inbreeding occurs when individual animals mate that are more closely related than would be the case if mating was random (Falconer & Mackay, 1996). There is a direct relationship between an increase in inbreeding and the reduction of heterozygosity for a given locus in a closed, unselected and panmictic population of finite size (Wright, 1931). The common practice in the selection of livestock, where animals are selected by truncation on estimated breeding values across age classes, results in increased genetic gains but will also lead to increased rates of inbreeding. This poses the threat of inbreeding depression that may hamper selection response and genetic diversity in the long run (Bijma *et al.,* 2001). Inbreeding and the rate of inbreeding (ΔF) also has an effect on the effective population size (N_e), for example the N_e based on ΔF among dairy cattle breeds in the United States were reported to be 161, 61, 65, 39 and 30 respectively for the Ayrshire, Brown Swiss, Guernsey, Holstein and Jersey populations (Weigel, 2001).

Shortening of the generation interval would afford the breeder more opportunities to select superior birds for economically important production and reproduction traits.

Earlier works reported numerous studies on the genetic parameters (Bunter & Cloete, 2004; Cloete *et al.,* 2006; 2008c) and selection responses (Cloete *et al.,* 2008b) for the production traits of a pair-bred ostrich flock at the Oudtshoorn Research Farm. However, no genetic variability analyses based on pedigree data have been done so far. It is known that the breeding structures in ostrich flocks are unlike that of other livestock, with confounding between random effects in a pair-bred population, as well as a very narrow male:female ratio (Cloete *et al*., 1998; 2008c). Awareness of the pedigree structure, levels of inbreeding and the effective population size of a local flock of ostriches can be used to avoid the possible loss of genetic variability and fitness (e.g. fertility) due to inbreeding when formulating modern breeding programmes for optimum production.

The aim of this study was thus to investigate the available pedigree structure, inbreeding levels, generation interval, effective population size and founder contributions of a well documented ostrich research flock. Knowledge of these parameters could help the industry when formulating breeding programmes.

2.2   Material and Methods

The pedigree data of a pair-breeding ostrich flock (n = 78 637), maintained at the Oudtshoorn Experimental Farm, South Africa, was used for this study. The data included records from 1978 to 2005. Each breeding pair was kept in a separate paddock to facilitate identifying parentage of the hatched chicks. Weights of laid eggs, parentage details, date of lay and day-old chick weight of all hatched eggs were recorded. Eggs were collected on a daily basis and incubated artificially. The general management of the breeding pairs, eggs and chicks has been described in detail by different authors (Van Schalkwyk *et al.,* 1996; Cloete *et al.,* 1998; Bunter, 2002; Cloete *et al*., 2006; 2008c).

The ENDOG software programme (version 4.8) (Gutiérrez & Goyache, 2005) was used for all genealogical analyses on the pedigree data. ENDOG is a population genetics computer programme that conducts several demographic and genetic analyses on pedigree data to monitor the changes in genetic variability and population

structure in a population, and can be freely downloaded from the World Wide Web at http://www.ucm.es/info/prodanim/html/JP_Web.htm#_Endog_3.0:_A

Several parameters were calculated for assessment of the concentration of the origin of animals and genes. The effective number of founders (f_e) was defined as the number of equally contributing founders that would be expected to produce the same genetic diversity in the population under study. For a given number of total founders, the more balanced their expected genetic contributions are, the higher the effective number of founders will be. The effective number of ancestors (f_a) (Boichard *et al.,* 1997) is the minimum number of ancestors (including founders and non-founders) explaining the complete diversity of the population. The "founder genome equivalent" (f_g) (Lacy, 1989) can be defined as the number of founders that would be expected to produce the same genetic diversity as in the population under study if the founders were equally represented and no loss of alleles occurred. The parameter f_g was obtained by the inverse of twice the average co-ancestry of the individuals included in a pre-defined reference population (Caballero & Toro, 2000). The reference population was defined as all animals with both parents known.

For assessing the completeness of the pedigree, ENDOG computes the following three traced generations for each animal in the pedigree:

(i)   Fully traced (complete) generations, which is defined as those separating the progeny of the furthest generation, where the 2nd generation ancestors of the individual are known. Ancestors with both parents unknown were considered as founders (generation 0).

(ii)   Maximum number of generations traced, defined as number of generations separating the individual from its furthest ancestor.

(iii)   Equivalent complete generations is computed for the pedigree of each animal as the sum over all known ancestors of the term $(1/2)^n$ where n is the number of generations separating the animal from each known ancestor (Maignel *et al.*, 1996; Boichard *et al.,* 1997).

The inbreeding coefficient (F_i) for each animal in the dataset was calculated according to the method of Meuwissen & Luo (1992). Individual inbreeding coefficients were used to compute the individual rate of inbreeding (ΔF_i) according to the methodology described by Gonzalez-Recio *et al.* (2007) and modified by Gutiérrez *et al*. (2009). The individual rate of inbreeding is an alternative measure of inbreeding, which is adjusted for the depth of the known pedigree. This coefficient

corrects the cumulative inbreeding coefficient F according to the pedigree depth of each animal. It is, however, not a measurement of inbreeding but an indicator of the increment in inbreeding for each animal, regardless of the number of generations known in its pedigree. Therefore, the individual rate of inbreeding makes it possible to distinguish between two animals with the same inbreeding coefficient but different number of generations over which inbreeding was accumulated (González-Recio *et al*., 2007; Gutiérrez *et al*., 2009). Slow inbreeding allows natural and artificial selection to operate and to remove the less fit animals. Less inbreeding depression among the individuals who accumulated the inbreeding over a larger number of generations are thus expected (Van Wyk *et al.,* 2009).

This coefficient should not be affected by a possible nonlinear increase of inbreeding over time, and thus, two animals with the same inbreeding coefficient could have a different inbreeding depression effects depending on the number of complete generations in their particular pedigrees (González-Recio *et al*., 2007).

The individual rate of inbreeding was calculated as $\Delta F_i = 1 - \sqrt[t-1]{1 - F_i}$, where F_i is the individual coefficient of inbreeding of an animal *i* and *t* is the "equivalent complete generations". The *t* was calculated using the ENDOG v 4.8 computer programme (Gutiérrez & Goyache, 2005). Using ΔF_i, ENDOG computes the effective population size (N_e) as $N_e = \frac{1}{2\Delta F_i}$ for each generation.

The average generation interval was calculated as the average age of the parents at the hatching of their selected progeny (James, 1977).

Trends were calculated for the average annual levels of inbreeding as well as for the rate of inbreeding using the regressions of applicable values on the year of hatch.

2.3   Results and Discussion

The progression of number of birds hatched per year is shown in Figure 2.1. A steep increase from 1990 to 1992 is evident, after which the number of birds in the population increased at a more gradual rate.

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Figure 2.1   Number of birds recorded per year of hatch from 1990 to 2005 for the Oudtshoorn resource ostrich flock

Parameters characterizing the genetic variability of the ostrich flock at the Oudtshoorn Research Farm are presented in Table 2.1. There were 253 equivalent founders (animals with one or more unknown parents) that contributed to the reference population in the original data set of 40 074 records. The effective number of founders for the reference population was 59, around 23% of the total number of founders. The reference population consisted of 39 784 birds hatched between 1990 and 2005. The number of ancestors responsible for 100% of the variation in the reference group was 267. However, 50% of that variation was explained by only 22 animals, and 20% by 6 ancestors. The animal with the largest individual contribution to the genetic make-up of the birds hatched between 1990 and 2005 was a single male responsible for 4.85% of the genetic variation.

Table 2.1 Parameters characterizing the probability of gene origin in the Oudtshoorn resource flock

Item	Total
Original dataset	40074
Reference population (both parents known)	39784
Number of founder animals (animals with one or more unknown parents)	253
Number of ancestors contributing to the reference population	256
Effective number of founder animals (f_e)	59
Effective number of ancestors (f_a)	58
Ancestors explaining 100% of genetic variability of population	267
Ancestors explaining 50% of genetic variability of population	21
Ancestors explaining 20% of genetic variability of population	6
Contribution of the main ancestor (%)	4.85
Average relatedness (%)	2.11
Maximum number of generations	2.70
Number of complete generations	1.81
Number of equivalent generations	2.17
Founder genome equivalent (f_g)	47.3

The ratio of f_e/f_a (1.02; Table 2.1), can be used to evaluate the loss in genetic variability available in the founders due to bottlenecks between the base population and the reference population. This ratio is an indication of the importance of bottlenecks in the development of the population. With a ratio close to unity, the population has been stable in terms of numbers of effectively contributing ancestors. If the ratio is larger than one, bottlenecks have played a role in the formation of the population (Sørensen *et al*., 2005). The number of founder genome equivalents (f_g) was 47.3, which is smaller than those estimated by f_e and f_a, as would have been expected. The number of founder genome equivalents account for, not only unbalanced contributions of parents to the next generation (as f_e and f_a) and for bottlenecks in the pedigree (as f_a), but also for the random loss of genes from parents to their offspring; therefore, f_g is always smaller than f_e and f_a, and decreases more rapidly over time. The degree to which the founder genome equivalent is smaller is an indication of the degree of random loss of alleles due to drift (Lacy, 1989; Tahmoorespur & Sheikhloo, 2011).

Pedigree completeness of the male and female lines up to three generations back is illustrated in Figure 2.2. The first ancestral generation, including all animals in the data set, was 99.3% complete. The second generation was 69% and 74% complete. The completeness decreased to 34% in the third generation.
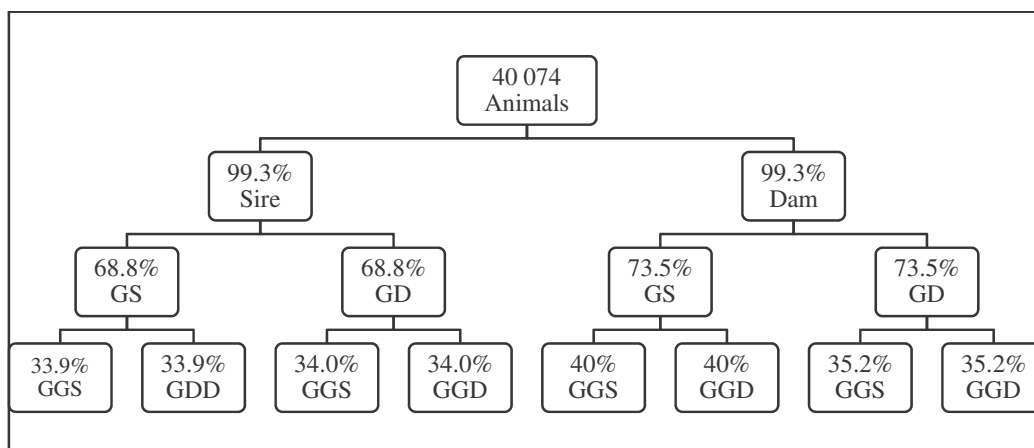
Figure 2.2 Level of pedigree completeness of the male and female lines up to three generations back

The numbers and proportions (%), relative to the full pedigree, as well as the mean level of inbreeding in an ostrich breeding flock is depicted in Table 2.2. When all the animals in the study were considered, the average inbreeding coefficient was 0.51%; compared to an average of 5.82% for inbred animals. As shown in Table 2.2 only 8.8 % of all the animals were inbred to some extent. No animals hatched before 1995 were inbred. The annual generation interval range of this flock (8.3 to 10.4) during this period was long (Fair *et al.*, 2006) resulting in few replacements being added to the flock per annum. It was thus easy to avoid the mating of related birds.

Table 2.2 Number (*n*) and proportion (%) of animals in full pedigree, and mean level of inbreeding (F)

	n	**Proportion (%)**	**F (%)**
Total number of animals	40 074	100.0	0.51
Non-inbred	36 221	90.4	0.00
Inbred	3 853	9.68	5.26

The trend depicting the average annual level of inbreeding for the ostrich flock under investigation is presented in Figure 2.3. The mean annual level of inbreeding was 0 % from 1990 to 1995, rising steadily from 1996 to 2005 at a rate of 0.10 % per annum to an average level of 1.2%. The increase in average annual inbreeding may be the result of a number of matings between close relatives in 2000 which resulted in

311 full sib, 363 half sib and 24 parent-offspring progeny. The current level of inbreeding in the flock is low and it should be possible to continue at relatively low levels, given sound mating management. It should however be kept in mind that inbreeding is likely to increase over time in a closed population of finite size.

y = 0.096x - 193.0
R² = 0.812
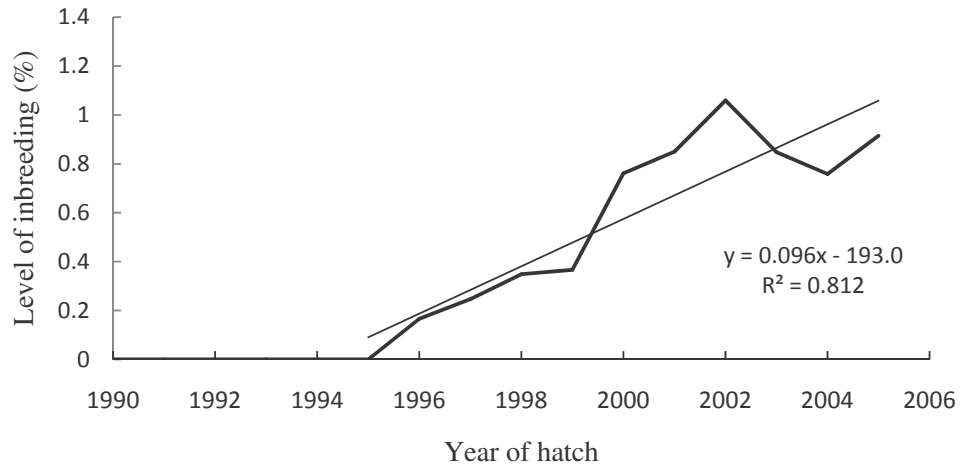
Figure 2.3   Mean annual level of inbreeding (%) by year of hatch

The trend of the annual individual rate of inbreeding (ΔF_i) for the ostrich flock under investigation is presented in Figure 2.4.

y = -0.066x + 132.6
R² = 0.659

y = 0.079x - 157.5
R² = 0.937
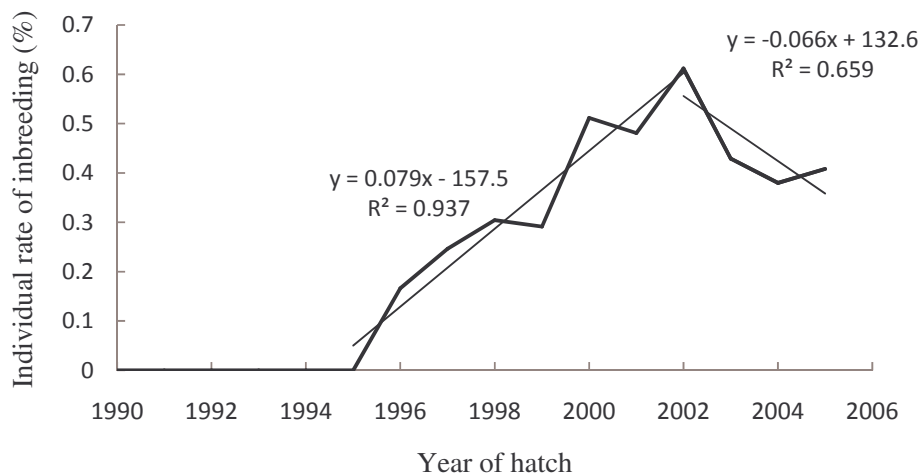
Figure 2.4   Mean annual individual rate of inbreeding by year of hatch

Similar to the trend in average annual level of inbreeding, a sharp increase is noticeable in the individual rate of inbreeding from 1996 onwards. This was at the stage when the selection lines reported by Cloete *et al.* (2008b) were formed. Initially inbreeding was not considered but was remedied when detected. Linear regressions of the individual rate of inbreeding on year of hatch resulted in estimates of the individual rate of inbreeding for the two distinct periods, 1995 – 2002 and 2003 - 2005 of 0.08 % and -0.07 % per year, respectively. The critical level of 0.5 % per year suggested for animal breeding programmes (Nicholas, 1989) is exceeded by the rate that was observed over the first period. During this period, three separate breeding lines were established, comprising of an unselected control line, a line selected for weight and a line selected for chick output (Cloete *et al.*, 2008b). As the lines were represented by relatively few animals (5-7 new breeding pairs introduced per line per year), inbreeding could have been expected to accrue, as with any population of finite size. However, estimates of the individual rate of inbreeding declined from 2003 to below 0.5% in 2003, 2004 and 2005 at an average rate of -0.07% per year. The reduction in the rate of inbreeding coincides with the introduction of unrelated breeding birds to the flock at the beginning of the 2003 breeding season (Cloete *et al.*, 2008b). Obtained ΔF_i values are still subject to change due to the relative shallowness of the analysed pedigrees (equivalent complete generations = 2.17) and more generations of pedigree data are needed to make proper use of this parameter. Cervantes *et al.* (2008) also reported that the trend of ΔF_i values tended to become more stable with the increase in t due to the correction resulting from deeper pedigrees of the individuals.

The estimate of effective population size (N_e) computed via the individual rate of inbreeding (Gutierrez *et al.,* 2008) for the current study was 112.7 animals, which is appreciably higher than the critical value of 50 animals suggested by the FAO (1998). Meuwissen (1999) stated that, due to mutation and drift, the critical N_e size should be between 50 and 100 animals. However, the method of calculating N_e can also have a substantial effect on the outcome. In the current study different N_e values were obtained using the three different methods of tracing generations in the pedigrees of animals, i.e. complete generations, maximum generations and equivalent complete generations and yielded N_e values of 73.65, 177.36 and 95.31 respectively. Furthermore, it should be noted that estimates of N_e are usually not constant and may change over time, given changes in average levels of inbreeding in the population,

generation interval and the number of known parents and progeny per parent; i.e. current estimates of N_e can decrease to below the critical value if the rate of inbreeding in the population should increase. Although the depth of the pedigrees and the levels of completeness of the pedigrees should be considered in making a comparison between different estimates of N_e, the estimated realised of effective population size of the ostrich flock at the Oudtshoorn Research Farm currently seem to be at acceptable levels.

Five forces are active in making the calculated N_e values using ΔF_i different from the real population size. These forces are: fluctuating population size, sex ratio of breeding animals, the Poisson distribution of family (offspring) numbers, overlapping generations (Felsenstein, 1971) and the spatial dispersion of the breeding population. Unlike dairy herds where the ratio of sires to dams is low, the sex ratio of ostrich breeding animals was close to 1:1 for all years under consideration, as would be expected in a pair-bred population (Cloete *et al.*, 1998; 2008b). Spatial dispersion also does not play a role in the flock as each male is paired off with a single female and is kept in a paddock that restricts interbreeding with other birds.

The calculated generation interval for the four gametic pathways were as follows: sire to son (7.74 ± 4.92 years), sire to daughter (7.77 ± 5.13 years), dam to son (7.50 ± 4.29 years), and dam to daughter (7.90 ± 4.79 years). The average generation interval of the reference population was 7.72 ± 4.79 years. This value is high and may hamper ostrich breeders from making reasonable genetic progress in the selection of production and reproduction traits. The average age of female and male breeding birds was however lowered intentionally in later years (Cloete *et al.*, 2006). Whereas breeding animals as old as 22 years were initially kept in the breeding flock, both male and female breeding animals are now culled at 10-11 years of age to help shorten the generation interval. This strategy was prompted by observed age trends in reproductive fitness, as described by Cloete *et al.* (1998) and Bunter (2002).

If it is considered that in excess of 200 000 slaughter birds are produced annually in South Africa (Brand & Jordaan, 2011), this flock is a miniscule sample of the total number of breeding ostriches found in South Africa. It can be speculated that the effective population size of South African ostriches is infinitely large and varied compared to other domestic livestock populations (particularly the dairy, beef and sheep populations).

2.4   Conclusions

Pedigree analysis was found to be useful in determining the status of genetic variability in the ostrich flock maintained at the Oudtshoorn Research Farm. The results showed a relatively low rate of inbreeding, resulting in a comparatively high effective population size. Inbreeding levels are currently low and manageable. However, the rather long generation interval of 7.7 years needs to be shortened to increase the rate of genetic improvement owing to more opportunities to select superior birds for economically important production and reproduction traits.

The individual rate of inbreeding that was obtained is still subject to change owing to the shallowness of the analysed pedigrees, and more generations of pedigree data is necessary to make proper use of this parameter. Follow-up studies are recommended for continued monitoring of the genetic variability in the flock and for the calculation of ΔF_i parameters as more data become available. The higher the numbers of generations in the pedigree, the more stable the genetic variability parameters are likely to become. It is concluded that the population investigated demonstrated acceptable levels of genetic variability.

3

ESTIMATION OF VARIANCE AND (CO)VARIANCE COMPONENTS FOR EGG WEIGHT, CHICK WEIGHT AND HATCHABILITY

3.1   Introduction

Prior knowledge of genetic parameters is necessary for compiling and designing breeding programmes (Bunter & Cloete, 2004). The magnitude of variance and (co)variance components will determine what traits will respond genetically to selection and how these traits are interrelated among themselves. Fixed effects affecting performance need to be considered before meaningful genetic improvement programmes can be embarked upon. The ostrich industry has not yet become part of the modern breeding world using mixed model methodology to estimate fixed effects and predict breeding values of individuals. There is an overall lack of knowledge of genetic and environmental influences in the industry (Cloete *et al.,* 2002). Current ostrich breeding / husbandry practices present challenges (Cloete *et al.,* 1998; Bunter & Graser, 2000), such as a lack of artificial insemination (AI), a lack of pedigree records due to communal nesting and the lack of any reliable mating and recording scheme.

The objective of this study was to estimate variance and (co)variance components for genetic effects and to quantify non-genetic effects affecting performance. Knowledge of these parameters could help in identifying selection objectives when creating breeding and mating programmes.

3.2 Material and Methods

3.2.1 Data

Pedigree and performance data for 71 147 individual egg records were obtained from a large pair breeding ostrich resource flock maintained at the Oudtshoorn Research Farm (ORF), near Oudtshoorn, South Africa. The data were collected from 1993 to 2005 and were the progeny of 414 dams and 441 sires, which were combined to form a total of 654 unique breeding pairs. The breeding flock mostly comprised of breeding animals belonging to the SA Black strain. A number of Zimbabwean Blue breeders have been introduced recently (Brand *et al.,* 2005; Cloete *et al.,* 2008a). However, these birds were represented only in the most recent production years (2003 and onwards). The study was thus confined to include only parents and progeny of the SA Black strain. Each breeding pair was kept in a separate breeding paddock to facilitate the identification of parentage. Eggs were collected daily, when available, and were recorded for egg weight (EWT), date of lay, paddock and parentage. The weight of all live day-old chicks (CWT) was also recorded for all chicks after being artificially incubated.

A detailed description of the general management of breeding pairs, eggs and chicks was given by Van Schalkwyk *et al.* (1996), Cloete *et al.* (1998) and Bunter (2002).

All analyses included the full pedigree file. The pedigree and structure of the data were fully discussed and analysed in Chapter 2.

The breeding season in Oudtshoorn generally comprises the months of June to January each year. There were some exceptions, i.e. the breeding season was extended to February during 1999 and some breeding pairs were paired off throughout the full year during 2002. The latter exception allowed a study on seasonal influences on ostrich reproduction (Lambrechts, 2004). The data from eggs produced in February 1999 and February to May of 2002 fell outside the normal breeding season (June to end January of the following year) and were thus edited from the data to exclude them from this study. These records comprised of 1 038 egg weights or <1.5% of the data. For the purposes of this research, data were available for the years from 1993 to 2005, while the months from June of the reference year to January of the

following year were represented annually. That is eggs laid in January were considered part of the preceding year's output.

Eggs produced by a specific breeding pair were sequenced chronologically within breeding seasons. Since a few male-female combinations produced more than 80 eggs in a breeding season, all eggs produced beyond the 80th egg were pooled. Eggs that were pooled made up 1.5 % of the total number of eggs being analysed.

Individual age was known for all parents included in the study. Initially male and female breeders were fairly old, reaching ages of 20+ years. The age structure of the breeding flock was changed from 1996, with fewer age groups to ensure a shorter generation interval (Cloete *et al.,* 2006). To facilitate analyses, birds with ages higher than 11 years were pooled for the purpose of this study. This change affected <13% of the eggs produced.

The data were edited to facilitate analyses of the following three traits assessed for individuals: EWT, CWT and hatchability (H). The EWT was the weight of eggs weighing 1000g or more (only eggs 1000g and heavier and that were not broken or cracked were set in the incubator). Eggs not set in the incubator comprised of less than 1.24% of the total number of eggs laid.

Eggs that were set in an incubator but did not hatch were assigned a 0 for the trait H and a 1 if the egg hatched. From the literature it is evident that about 50% of ostrich eggs eventually hatch when incubated artificially (Deeming & Ar, 1999; Bunter & Cloete, 2004). Set eggs that failed to hatch could either have been infertile or dead in shell.

3.2.2 Statistical analyses

The software package ASREML (Gilmour *et al*., 2006) was used for single-trait animal model analyses of EWT, CWT and H with the egg or chick treated as the individual. The software allows the estimation of various random effects under an animal model, and also predicts least squares means for selected fixed effects. Longitudinal data such as age and seasonal trends can be modelled, using cubic splines, as described by Verbyla *et al*. (1999). Fixed effects were tested at the α = 0.05 level with numerator degrees of freedom (df) of (*n*-1) where *n* corresponded to the levels of the particular fixed effect and denominator (error) df taken as infinity.

The fixed effects of year (1993 to 2005), month (June to January), the year by month interaction, age of service sire and dam (2 to 11+ years of age), sire and dam age interaction, year of egg and chick production (1993 to 2005) was combined with some nutritional experimental groups over the said period, to form 44 contemporary groups (CG). The temporal sequence of the egg laid within season (1st egg to 80th + egg) was tested for significance and possible inclusion in the single-trait models. The random effect of spline sequence was considered for inclusion in the model. The addition of the random spline sequence effect was considered as a "fixed" environmental effect. These effects were represented by β in Model 1.

A simple fixed effects model plus random spline sequence was run using ASREML to test significance of effects.

$$y_i = X\beta + e \qquad .... (1)$$

where

y_i was a vector of observations for each the three traits EWT, CWT and H,

X   was an incidence matrix relating records to the fixed effects β and

e   was a vector of residuals.

SAS was used to plot a graph of significant interaction between fixed effects of month by year and are presented in Figures 3.1. A 3-dimensional plot and smoothing regression programme were used to generate the interaction graph.

After determining significance of the fixed effects, seven random effects were considered for inclusion in three single-trait animal models. The seven random effects considered were firstly the random genetic effect of, direct (a) and maternal (m) and then the environmental effects of, common environment of the dam by year (ce), permanent environmental effect of unique hen over years (pe), and finally the random environmental effect of the breeding paddock (bp). The random effect of the service sire (ss) which was the mate of the hen was only included in models tested for hatchability.

The random effects were added to the fixed effects models, starting direct genetic effect a, to test for significance for possible inclusion in the model. If

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significant the model would be considered the better model for prediction purposes. The maternal genetic effect, ce, pe, and bp were each added in turn ending with Model 6. The models are listed below with model number in parentheses and the number of random effects (*nR=*) in italics:

$$y_i = X\beta + e \qquad\qquad (1) \qquad nR=1$$

$$y_i = X\beta + Z_1a + e \qquad\qquad (2) \qquad nR=2$$

$$y_i = X\beta + Z_1a + Z_2m + e \qquad\qquad (3) \qquad nR=3$$

$$y_i = X\beta + Z_1a + Z_2m + Z_3ce + e \qquad\qquad (4) \qquad nR=4$$

$$y_i = X\beta + Z_1a + Z_2m + Z_3ce + Z_4pe + e \qquad\qquad (5) \qquad nR=5$$

$$y_i = X\beta + Z_1a + Z_2m + Z_3ce + Z_4pe + Z_5bp + e \qquad (6) \qquad nR=6$$

where y_i was a vector of observations for the ith trait, X was an incidence matrix relating records to the fixed effects (β); Z_1, Z_2, Z_3, Z_4, and Z_5, were incidence matrices relating records to the additive genetic effects (Z_1), genetic maternal effects (Z_2); common environmental effect of the dam within year effects (Z_3), permanent environmental effect of unique hen over years (Z_4) and breeding paddock effect (Z_5) and a, m, ce, pe, bp and e were vectors of direct genetic, maternal genetic, common environmental, permanent environmental, breeding paddock and residual effects, respectively. Under an animal model it was assumed that: $Var(a) = A\sigma^2_a$ and $Var(m) = A\sigma^2_m$ where A is the Numerator Relationship Matrix. The remaining effects were assumed to be distributed as $Var(ce)= I\sigma^2_{ce}$; $Var(pe)= I\sigma^2_{pe}$, $Var(bp)= I\sigma^2_{bp}$, and $Var(e)= I\sigma^2_e$ where I = identity matrices of order equal to the number of hens x year, number of hens, number of breeding paddocks, and number of records respectively, and σ^2_a, σ^2_m, σ^2_{ce}, σ^2_{pe}, σ^2_{bp} and σ^2_e were direct genetic variance, maternal genetic variance, common environmental variance (hen within year), variance due to permanent environment (hen over years), breeding paddock variance and environmental (residual) variance respectively.

Convergence was considered to have been obtained when the Log-likelihood changed less than 0.002 and the individual variance parameter estimates changed less than 1% (Gilmour *et al.*, 2006). Tests of significance of each random effect were

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performed using log likelihood ratio tests. An effect was regarded as significant when its inclusion in the model caused a significant increase in the log likelihood. When twice the difference between log likelihoods for two models being considered were greater than 3.841 (Chi-square critical test statistic) the inclusion of the effect was considered significant. When differences between log likelihoods were not significant the model with the fewest random effects were chosen. Alternatively, for two models with the same number of random terms, and assuming identical fixed effect modelling, the model with the higher Log-likelihood was considered superior.

Two-trait analyses with covariance structures were used to estimate variance and co-variance parameters and ratios for EWT, CWT and H. Starting values used in the two-trait analyses were obtained from the single-trait analyses. An animal model with random effects a, m, ce, pe, bp and e (according to the values) was used for both the single- and two-trait analyses. The fixed effects were the same as discussed in the single-trait models.

The relationship between EWT and H was further explored by categorizing EWT into 100g weight categories. This relationship was presented graphically.

3.3 Results and Discussion

3.3.1 Descriptive statistics

Descriptive statistics of egg, chick and hatching data after editing are presented in Table 3.1. There were 69 240 eggs that weighed 1000g or more that were incubated, less than 1.24% were not incubated due to infertility or broken shells. The mean weight was 1 431g for EWT and 863g for CWT with low coefficients of variation (CV) of 9.5% and 11.8% respectively. These CV's corresponding with values of 9.9% and 11.7% reported by Bunter (2002). The mean CWT was 60% of the mean EWT. This was expected as chicks with less than ± half their egg weights have a higher mortality or compromised survival rate (Brand *et al.,* 2007).

Table 3.1 Descriptive statistics of egg and chick weight, and hatching data after editing

Trait	n	Phenotypic mean	SD	Minimum	Maximum	CV (%)
EWT (g)	69 240	1 431.11	136.27	1 000	2 120	9.5
CWT (g)	35 257	863.48	101.53	445	1 332	11.8
H	35 257	0.503				

EWT	=	Egg weight of eggs weighing 1000g or more (only eggs 1000g and heavier were set)
CWT	=	Chick weight of live day-old chicks
H	=	Eggs that hatched (eggs that did not hatch could have been broken, under weight for setting, infertile or dead-in-shell)
SD	=	Standard deviation

Of the 70 109 eggs laid 50.3% hatched. The 49.7% that did not hatch were due to shells being compromised, eggs too light for setting, eggs that were infertile or died in shell prior to or during hatching. Hatchability reported by Deeming & Ar (1999) for a limited number of commercial farms operating in new industries ranged from 3.3 to 80%. Definitions of hatchability vary from percentage of eggs hatched that were laid to percentage of eggs hatched that were fertile and set in the incubator. Eggs that do not meet weight and size requirements and that show signs of compromised shells are generally not set in the incubators (Brand *et al.,* 2007). Eggs identified as being infertile when candled at 14 to 21 days of incubation are removed from the incubators. Table 3.2 summarises some reported hatchability percentages from various countries.

Table 3.2 Summary of reported hatchability of ostrich eggs in different countries

Country	Range of hatchability (%)	Reference
94 Australian farms	51-70	Badley (1997)
12 Australian farms	67-68	More (1996)
21 Countries	17-99 (mean=63.8)	Bunter & Graser (2000)
	62	Van Schalkwyk *et al.* (1996)
1 SA research station	42-59	Bunter (2002)
	50	Present study (2012)

Hatchability = percentage of eggs hatched that were laid or percentage of eggs that hatched that were fertile and incubated (different definitions in hatchability result in a range given from one research station)

3.3.2 Fixed effects from single-trait analyses

The fixed effects of year (1993 to 2005), month (June to January of the following year), year by month interaction, age of dam (fage) (2 to 11+ years of age), CG and sequence of the egg laid within season (1st egg to 80th + egg) were all significant (P<0.05) and retained in subsequent analyses (Table 3.3). Spline (seq) expressed as a ratio of the phenotypic variance for EWT and CWT explained 1% or less of the observed variation although significant this factor was not included in the models for analysis.

Table 3.3 Significance of fixed effects according to the analyses of variance for egg weight (EWT), chick weight (CWT) and hatchability (H)

Source (fixed effects)	df	EWT	CWT	H
Year	12	***	***	***
Month	7	***	***	***
Year x month	84	***	***	***
Female age (fage)	9	***	***	***
Linear Sequence	1	***	***	***
Contemporary group	38	***	***	***

df = degrees of freedom, *** P<0.001; * P<0.05

The interaction effect of year by month on EWT is presented in Figures 3.1. From Figure 3.1 it can be seen that in general heavier eggs are laid towards the end of the season with lighter eggs occurring earlier in the season, while EWT generally declined over the 13-year period studied.
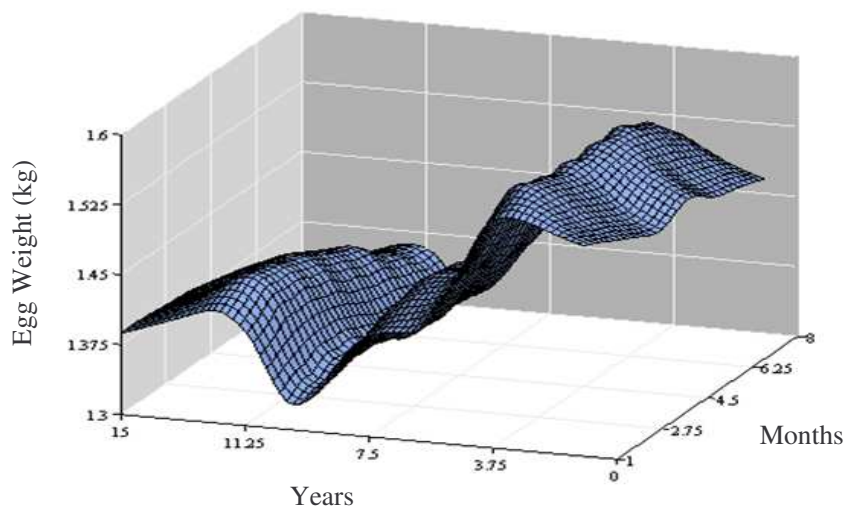
Figure 3.1 Three-dimensional graph of the year x month interaction effect on EWT

3.3.3 Random effects

Log-likelihoods obtained for EWT and CWT under the different models fitted, with the most appropriate model shown in bold, are given in Table 3.4. The Log-likelihoods for hatchability are given in Table 3.5. The resultant variance components and ratios of the random effects for the three traits are shown in Tables 3.6, 3.7 and 3.8 respectively.

Model 6 fitted the data best for EWT. The trait CWT was similar however, Model 5 (addition of pe) was not significantly different to Model 4 according to changes in Log-likelihood giving rise to a seventh model being tested where pe was dropped and bp was added to Model 4 instead. This indicated that the permanent hen effect was not significant for CWT but did play a role in EWT (Table 3.4).

Model 6 for EWT included the fixed effects as discussed above and the random direct genetic effect, maternal genetic effect as well as the random effects of common environment, permanent environment and breeding paddock.

Table 3.4   Log-likelihoods obtained for the 6 models tested for egg weight (EWT) and day-old chick weight (CWT)

Model	*nR*	EWT	CWT
1	1	106 852.66	63 956.77
2	2	137 731.79	76 232.18
3	3	139 706.96	77 251.04
4	4	144 001.12	78 191.94
5	5	144 004.07	78 193.26
6	6	**144 383.98**	**78 211.43**
7	5	-	78 210.41*

nR	=	number of random effects in the model tested
Model	=	model number as described in material and methods
EWT	=	Egg weight of whole eggs (not broken) weighing 1000g or more
CWT	=	Chick weight of live day-old chicks
*	=	Model 7 for CWT did not include the random effect of permanent environment (inclusion of this effect in Model 5 was not significantly better than Model 4) indicating that the permanent hen effect is not significant for CWT but did play a role in EWT

The best operational model for H as shown in Table 3.5 included the same fixed effects as discussed above with the random direct genetic effect, maternal genetic effect as well as the random effects of service sire. The addition of the random effect of pe was not significant and thus not included in the model.

Table 3.5   Log-likelihoods obtained for 6 different models tested for hatchability (H)

Model	*nR*	Random effect	LL
1	1	Error variance	14 504.40
2	2	Error + direct animal	18 218.46
3	3	Error + direct animal + maternal	18 286.91
4	3	Error + direct animal+ service sire	18 307.24
5	**4**	**Error + direct animal+ maternal + service sire**	**18 340.21**
6	5	Error + direct animal+ maternal + service sire + pe	18 334.13

nR	=	number of random effects in the model tested
Model	=	model number
H	=	Hatched chicks (0/1)
LL	=	Log-likelihood
pe	=	Permanent environment

3.3.2.1 (Co)variance components and ratios

Variance components and ratios for EWT are shown in Table 3.6 for all models fitted. Presenting the results of the model in this manner, allows the opportunity to examine how the introduction of random effects partitioned and adjusted existing variance components, when added to the model. The variance components with their resultant ratios and standard errors (SE) in bold are shown for all models. This procedure was repeated for CWT and H in Tables 3.7 and 3.8 respectively.

Changes in variance ratios due to additional random effects being added to the models are of interest and indicate that for the trait EWT if only direct additive and maternal genetic effects were used as random effects (Model 3) both effects would be overestimated, 27% and 62% instead of 12% and 27% respectively.

The direct additive and maternal genetic effects for Model 6 amounted to 12% and 27% respectively. The h^2 value was slightly lower than the 19% reported by Bunter & Cloete (2004), but m^2 was similar to the value of 31% reported by the latter authors. It should be considered that the present analysis included slightly different modelling (fixed and random) compared to that of Bunter & Cloete (2004), which could have contributed to these differences. The present data set also spanned more years with some changes having been made to the age structure of the breeding pairs, in an attempt to shorten the generation interval, which could also have had some influence on the results. Ratios of 9% and 22% for ce and pe respectively added up to slightly higher than the previous value of 24% reported by Bunter & Cloete (2004) for pe only. The variance ratio of paddock of 11% was similar to the figure of 13% reported by Bunter & Cloete (2004).

The residual variance expressed as a ratio of phenotypic variance was 20% suggesting that a large proportion (80%) of the variation in EWT has been accounted for by the components in the model.

Table 3.6   Variance components and **ratios (± SE)** for EWT (kg)

Model	Log-likelihood	Model improvement in LL	Residual	a	m	ce	pe	bp	p
1	106852.66	0	0.016						
2	137731.79	61758.26	0.0028	0.0075					0.0103
			0.28 ± 0.0086	**0.72 ± 0.0086**					
3	139706.96	3950.34	0.0027	0.0069	0.016				0.025
			0.11 ± 0.0107	**0.27± 0.0199**	**0.62 ± 0.0197**				
4	144001.12	8588.32	0.0030	0.0044	0.0127	0.0020			0.022
			0.14 ± 0.0161	**0.20 ± 0.027**	**0.58 ± 0.0237**	**0.09 ± 0.0065**			
5	144004.07	5.9	0.0031	0.0043	0.0068	0.0020	0.0037		0.020
			0.15 ± 0.0185	**0.22 ± 0.0300**	**0.34 ± 0.0845**	**0.10 ± 0.0075**	**0.18 ± 0.0698**		
6	**144383.98**	759.82	0.0039	0.0023	0.0055	0.0019	0.0045	0.0021	0.020
			0.20 ± 0.0183	**0.12 ± 0.0286**	**0.27 ± 0.0811**	**0.09 ± 0.0068**	**0.22 ± 0.0685**	**0.11 ± 0.0169**	

Each model besides Model 1 has its variance components (σ^2) above with their resultant heritabilities / **ratios and ± standard errors (SE) below in bold**.
Model improvement in LL = 2 x the difference between the Log-likelihoods of successive models
EWT = egg weight (kg) of eggs weighing 1000g or more
a   = animal genetic effect
m   = maternal genetic effect
ce = common environment
pe = permanent environment
bp = breeding paddock
p   = phenotypic

Table 3.7   Variance components and ratios (± SE) for CWT (kg)

Model	Log-likelihood	Model improvement in LL	Residual	a	m	ce	pe	bp	p
1	63956.77	0	0.0094						
2	76232.18	24550.82	0.0020	0.0050					0.007
			0.28 ± 0.0119	**0.72 ± 0.0119**					
3	77251.04	2037.72	0.0023	0.0037	0.0070				0.013
			0.18 ± 0.0183	**0.28± 0.0284**	**0.54 ± 0.0235**				
4	78191.94	1881.8	0.0027	0.0022	0.0061	0.00078			0.012
			0.23 ± 0.0220	**0.19 ± 0.0336**	**0.52 ± 0.0262**	**0.07 ± 0.0053**			
5	78193.26	2.64	0.0027	0.0022	0.0042	0.00078	0.0012		0.011
			0.24 ± 0.0246	**0.20 ± 0.0359**	**0.38 ± 0.0795**	**0.07 ± 0.0059**	**0.11 ± 0.0615**		
7	78210.41	36.94 *(comparing model 7 vs. 4)*	0.0030	0.0015	0.0059	0.00073	-	0.00046	0.012
			0.26 ± 0.0221	**0.13 ± 0.0331**	**0.51 ± 0.0273**	**0.06 ± 0.0052**	**-**	**0.04 ± 0.0099**	
6	78211.43	2.04 *(comparing model 6 vs. 7)*	0.0030	0.0015	0.0042	0.00073	0.0011	0.00046	0.011
			0.28 ± 0.0247	**0.14 ± 0.0352**	**0.38 ± 0.0793**	**0.07 ± 0.0058**	**0.10 ± 0.0609**	**0.04 ± 0.0011**	

Each model besides Model 1 has its variance components (σ^2) above with their resultant heritabilities / **ratios and ± standard errors (SE) below in bold**

Model improvement in LL = 2 x the difference between the Log-likelihoods of successive models

CWT	=	chick weight (kg) of live day-old chicks

a	=	animal genetic effect	bp	=	breeding paddock
m	=	maternal genetic effect	p	=	phenotypic
ce	=	common environment	pe	=	permanent environment

Model 5 was not significantly better than Model 4 thus a seventh model was tested which included the random effect of breeding paddock, this inclusion was significantly better than Model 4. Model 6 was then fitted to test the addition of pe to Model 7. This inclusion was not significantly better than Model 7 however Model 6 was used for CWT (Table 3.7) as this allows for the partitioning of the variance components to reflect those used in EWT. The result for Model 6 for h^2 (14%) accorded with that of Bunter & Cloete (2004) (16%) but m^2 was substantially higher in the present study (38% vs. 26%). The reasons as cited for Table 3.6 for differences between authors also apply to Table 3.7. Low variance ratios of 7% and 10% were obtained for ce and pe respectively. The variance ratio of 4% for paddock was similar to the variance ratio of 5% reported by Bunter & Cloete, (2004). The residual variance expressed as a ratio of phenotypic variance was 28% showing that a large proportion of the variation (72%) in CWT has been accounted by the model.

Hatchability was defined as the percentage of day-old chicks that hatched from the eggs that were set. The h^2 estimate for H amounted to 9%, while m^2 of 13% was observed (Table 3.8). The variance ratios attributed to ss was 8. The large proportion of the phenotypic variation attributed to random error (70%) could be largely due to the binary nature of H. Nevertheless it is interesting to note that H was heritable, suggesting that selection for hatchability would result in genetic gains. The frequency of hatched chicks was ~50%, and therefore the statistical assumptions of normality for the analyses of the binary data remain unchanged. When the binomial probability histogram for binary data is not too skewed the normal distribution is expected to approximate the binary trait (Devore, 2000). The central limit theorem shows that as sample size and the number of samples increase the normal distribution approximates the binomial distribution (Guerra, 2004).

Estimates of genetic parameters for EWT, CWT and H under the best model are presented in Table 3.9. All traits exhibited a significant (more than twice the corresponding SE) level of additive genetic variance suggesting EWT, CWT and H would respond to selection pressure. Whether one would want to increase or decrease egg and chick weights would depend on correlations with subsequent growth and other economically important traits.

Table 3.8   Variance components and ratios (± SE) for H

M	LL	MILL	Residual	a	m	ss	pe	p
1	14 504.40	0	0.2397					
2	18 218.46	7428.12	0.1247	0.1727				0.2974
			0.42 ± 0.0232	**0.58 ± 0.0232**				
3	18 286.91	136.9	0.1497	0.1208	0.0339			0.3044
			0.49 ± 0.0265	**0.40± 0.0320**	**0.11 ± 0.0154**			
4	18 307.24	177.56	0.1445	0.1309		0.0211		0.2965
			0.49 ± 0.0288	**0.44± 0.0323**		**0.07 ± 0.0101**		
5	18 340.21	65.94	0.1966	0.0261	0.0373	0.0215		0.2815
			0.70 ± 0.0287	**0.09 ± 0.0423**	**0.13 ± 0.0176**	**0.08 ± 0.0115**		
6	18 334.13	*ns*	0.2008	0.0176	0.0000	0.0230	0.0261	0.2676
			0.75 ± 0.0248	**0.07 ± 0.0353**	**0.00 ± 0.0000**	**0.09 ± 0.0116**	**0.10 ± 0.0126**	

Each model besides Model 1 has its variance components (σ^2) above with their resultant heritabilities / **ratios and ± standard errors (SE) below in bold.**
Model improvement in LL = 2 x the difference between the Log-likelihoods of successive models
H   =   hatchability (0/1)
a   =   animal genetic effect
m   =   maternal genetic effect
pe   =   permanent environment
p   =   phenotypic
ns   =   non significant improvement in log-likelihood

Table 3.8   Estimated variance components and ratios (± SE) of EWT, CWT and H

	EWT	CWT	H
Variance components			
direct additive genetic	0.0023	0.0015	0.0261
maternal genetic	0.0055	0.0042	0.0373
common environment (hen within year)	0.0019	0.0007	-
permanent environment (hen over years)	0.0045	0.0011	-
breeding paddock	0.0021	0.0005	
Service sire	-	-	0.0215
residual	0.0039	0.0030	0.1966
Variance ratios			
h^2	0.12 ± 0.029	0.14 ± 0.035	0.09 ± 0.042
m^2	0.27 ± 0.081	0.38 ± 0.079	0.13 ± 0.018
c^2_{ce}	0.09 ± 0.007	0.07 ± 0.006	-
c^2_{pe}	0.22 ± 0.069	0.10 ± 0.061	-
c^2_{bp}	0.11 ± 0.017	0.04 ± 0.001	-
c^2_{ss}	-	-	0.08 ± 0.012
c^2_{e}	0.20 ± 0.018	0.28 ± 0.025	0.70 ± 0.029

Hatchability = eggs that were laid that hatched and survived to day-old chicks
h^2 =   direct heritability
m^2 =   maternal heritability
c^2_{ce} =   common environment variance as a proportion of phenotypic variance
c^2_{pe} =   permanent environment variance as a proportion of phenotypic variance
c^2_{bp} =   paddock common environment variance as a proportion of phenotypic variance
c^2_{ss} =   Service sire, mate of the hen
c^2_{e} =   environmental (residual) variance as a proportion of phenotypic variance

The maternal genetic effects were high for EWT and CWT (Table 3.8). However there was no maternal variation for H. Resultant h^2 were moderate to high for EWT and CWT and would also respond to selection pressure. The ratio for common environment (hen within a year) was virtually constant for the three traits at 9%, 7% and 8% respectively. The permanent environmental effects of hen over years were respectively 19%, 10% and 7% for EWT, CWT and H. Residual variance is shown as a ratio of phenotypic variance (c^2_e) and amounted to respectively 19% and 28% for EWT and CWT but a high 74% for H.

3.3.4 (Co)variance ratios for two-trait analyses

Two-trait analyses with covariance structures added were used to estimate variance and co-variance parameters for EWT, CWT and H. Variance ratios in bold on the diagonals and correlations are shown in Table 3.10. Two-trait heritability estimates were largely similar to those from the single-trait analyses.

Table 3.10   (Co)variance ratios for EWT, CWT and H. Variance ratios are on the diagonal with covariance ratios above the diagonals

Traits	EWT	CWT	H
Additive genetic correlations (h^2 in bold)			
EWT	**0.10 ± 0.03**	1.00 ± 0.02	-0.08± 0.19
CWT		**0.13 ± 0.04**	-0.22± 0.18
H			**0.09 ± 0.02**
Maternal genetic correlations (m^2 in bold)			
EWT	**0.31 ± 0.08**	0.96 ± 0.02	0.00± 0.00
CWT		**0.38 ± 0.08**	0.00± 0.00
H			**0.00 ± 0.00**
Temporary environmental correlations (c^2_{ce} in bold)			
EWT	**0.09 ± 0.01**	0.92 ± 0.01	0.10 ± 0.04
CWT		**0.07 ± 0.01**	0.16± 0.05
H			**0.08 ± 0.005**
Permanent environmental correlations (c^2_{pe} in bold)			
EWT	**0.19 ± 0.07**	0.89 ± 0.05	0.20 ± 0.16
CWT		**0.10 ± 0.06**	0.20 ± 0.22
H			**0.07 ± 0.01**
Breeding paddock correlations (c^2_{bp} in bold)			
EWT	**0.10 ± 0.02**	0.98 ± 0.01	0.48± 0.16
CWT		**0.03 ± 0.01**	0.60± 0.19
H			**0.015 ± 0.01**

EWT = egg weight of eggs weighing 1000g or more
CWT = live day-old chick weight
H   = eggs that were laid that hatched and survived to day-old chicks
h^2 = direct heritability
m^2 = maternal genetic as a ratio of phenotypic variance
c^2_{pe} = permanent environment as a ratio of phenotypic variance
c^2_{bp} = breeding paddock as a ratio of phenotypic variance
c^2_{ce} = common environment as a ratio of phenotypic variance

Genetically EWT and CWT were the same trait both on the direct and maternal genetic levels (Table 3.10). These high correlations accord with those of 0.95 and 0.96 for additive and maternal correlations between EWT and CWT reported by Bunter & Cloete (2004). Therefore egg weights to a large extent determine chick weights. H was largely unrelated to EWT and CWT at all levels (r of 20% or below). Moderate genetic changes in EWT are therefore unlikely to have a large impact on H. At this stage it is appropriate to gain a better insight into the exact relationship of H with EWT.

Because of the difficulty of optimising incubation management for all egg weights, eggs weighing below 1000g and above 2000g are not set in the incubator. These cut off weights were set based on practical experience of the management staff. The 0% H for very light eggs (< than 1000g) and heavy eggs (> 2000g) is thus expected however Figure 3.3 indicates that eggs weighing between 2000 and 2100g would have mean hatchability's of 37%. Eggs weighing between 1300g and 1800g were most likely to hatch (51-54% hatchability). The trend fitted, of a second order polynomial to the data, had R^2 = 97 % indicating a reasonably good fit. Egg numbers were not shown but were considerably less in the tail regions of the figure than in the central region. Selection for an optimum weight should be encouraged as incubator conditions are optimal for intermediately sized eggs. Optimum weight ranges are common among animal species and typically exhibit lower survival for extremes.

The equation shown on the figure: $y = -1.3247x^2 + 19.267x - 14.846$, $R^2 = 0.9679$
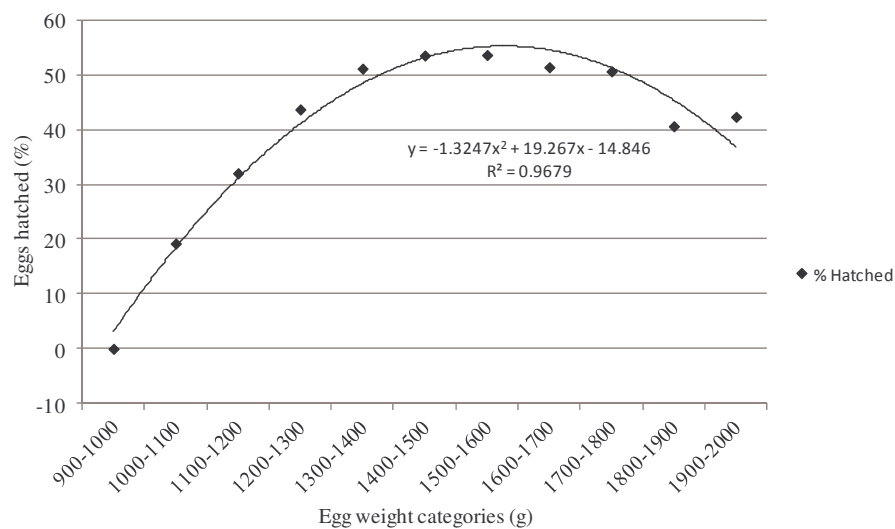
Figure 3.3   Percentage of eggs hatched per egg weight category

3.4   Conclusions

This study demonstrated that the fixed effects of year, month and their interaction year x month, sire and dam age and the interaction sire x dam age, sequence the egg was laid in and contemporary group contribute significantly to the traits measured. These effects should thus be included in models to ensure accurate genetic parameters. All traits exhibited genetic variation and should respond to directed selection. The random environmental effects of ce, pe and bp were low in magnitude but also significant indicating their inclusion in genetic models. EWT and CWT was highly correlated at all levels as was expected. However, neither weight trait was correlated with H suggesting that H could be improved independently.

PARAMETER ESTIMATES FOR REPRODUCTIVE OUTPUT AND PRODUCT QUALITY TRAITS OF OSTRICH FEMALES WITHIN BREEDING SEASONS

4.1   Introduction

Guidelines for selection to improve egg and chick production in the commercial ostrich industry should be based on knowledge of genetic parameters of these important economic production traits. Several factors such as colony mating, shared nests, small flocks without genetic ties and that pairs are mated for life, have stemmed progress in estimating genetic parameters for the ostrich industry (Bunter & Cloete, 2004). It could be argued that experience from the well developed and advanced poultry industry could assist and be a guideline for the ostrich industry. The poultry industry cannot, however, act unconditionally as a template or role model for the ostrich industry (Bunter & Cloete, 2004).

Annual genetic improvement is particularly impressive in the more intensive animal production industries (poultry, dairy cattle and pigs), due in part to their use of modern breeding techniques to identify superior parents, modern breeding programmes and well defined breeding objectives. These techniques could be used to modernize the ostrich industry although genetic and environmental influences on production are largely unknown in the industry. Moreover, defined breeding objectives and industry breeding structures in the ostrich industry are absent. An overview of recent progress made on the genetic basis of ostrich production traits was presented in a review by Cloete *et al*. (2008c) thus adding to the knowledge base for the industry.

Considering that meat and leather are the main sources of revenue for ostrich farmers, it is evident that egg and chick output (hereafter termed as reproduction)

should form an integral part of the selection objective for this species (Cloete *et al*., 2002). Annual reproduction, over an 8-month breeding season was shown to be heritable (Bunter *et al*., 2001a; Cloete *et al*., 2004), while responses to selection for egg and chick production, based on the maternal phenotype, has also been reported (Cloete *et al*., 2004; 2008b). It is known that ostrich reproduction is affected by hen age (Bunter, 2002; Lambrechts, 2004), with 2-year old ostriches generally producing fewer eggs or chicks than their mature contemporaries. Reproduction in ostriches also follows a distinctive seasonal pattern over the production season (Lambrechts, 2004). Research was directed at the derivation of age specific seasonal trends for reproduction in ostriches (Fair *et al*., 2005). This information was required to act as a guideline pertaining to the earliest age for selection on own performance in this species.

Advances in computers and computer software programmes facilitate the analyses of more complicated, larger data sets and models, allowing researchers to include new parameters on larger more recent data sets. Studies are thus required to investigate the relationships between repeated cycles of reproduction within a season and over years, to ascertain whether adequate genetic variation for accurate selection of superior animals is present early in the reproductive life of the animals. Early identification and use of high performance breeders would improve the production of the flock by shortening the generation interval and replacing parents with genetically improved offspring.

The flock has been studied previously by Bunter (2002), Cloete *et al*. (1998) and Fair *et al.* (2005). Each study, although done on the same flock, is unique in the sense that more data were available at each opportunity. A further updated analysis for the flock was considered important especially in view of improvements in methodology to fit additional random factors.

The aim of this study was to estimate genetic and environmental parameters for egg and chick production, mean egg and day-old chick weights and hatchability within breeding seasons. Knowledge of these parameters could help the industry when formulating breeding programmes for optimum production.

4.2   Material and Methods

Data of pedigree and performance for 78 632 individual egg records were obtained from a large pair breeding flock maintained at the Oudtshoorn Research Farm formerly known as the Klein Karoo Agricultural Development Centre (KKADC), South Africa. These eggs were collected from 1991 to 2005 and were the progeny of 406 females and 436 males comprising 654 breeding pairs. All breeding pairs were kept in separate breeding paddocks to facilitate parentage identification of the offspring. Weights of laid eggs, parent details, date of lay and day-old chick weight of all hatched eggs were recorded. Eggs were collected daily and incubated artificially. The general management of breeding pairs, eggs and chicks has been described in detail (Van Schalkwyk *et al.,* 1996; Cloete *et al.,* 1998; Bunter, 2002).

These data were used to construct five traits to be analysed which were all treated as traits of the hen:

(1)   Egg production (EP): Total number of eggs laid per month per hen.

(2)   Chick production (CP): Total number of chicks hatched per month per hen.

(3)   Mean egg weight (MEW): (Total weight of eggs laid per month per hen) / EP

(4)   Mean day old chick weight (MCW): (Total weight of day-old chicks hatched per month per hen) / CP

(5)   Percentage hatched (H): (CP / EP) x 100.

The 78 632 individual egg records were edited to form 13 876 hen-by-month records. The ages of the individual hens and sires ranged from 2 to 20 years for hens and 2 to 21 years for sires. After preliminary analyses it was decided to pool the data to form seven new age categories. The ages were pooled as the quantity of egg and chick weight data for these older birds were limited resulting in sparse and insufficient data for some classes of calendar month by hen age. Fixed effects considered comprised of seven categories (2, 3, 4, 5, 6-7, 8-11, and 12+ year olds) of hen and sire age, year of egg and chick production (1991 to 2005) was combined with some nutritional experimental groups, as well as some ostrich genotypes (Zimbabwe Blacks and Reds and SA Blues) to form 47 contemporary groups (CG), month by hen age interaction and the month by CG interaction. These effects were included in all analyses. Number of production days was also included as a linear covariate for the quantitative (EP and CP) and the qualitative (MEW, MCW and H) traits as not all

hens had equal number of days to breed due to random deaths, throughout the breeding season, of male and female birds. The breeding season had eight months comprising of June of a present year to January of the following year. June, July and August being winter with spring in September, October, and November followed by the summer months of December and January as Oudtshoorn, South Africa is located in the Southern hemisphere.

ASREML (Gilmour *et al.*, 2006) was used to estimate (co)variance components for each trait. The software allows the estimation of various random effects under an animal model, and also predicts least squares means for selected fixed effects. Fixed effects were tested at the $\alpha = 0.05$ level with numerator degrees of freedom (df) of (n-1) where n was the number of levels of each fixed effect.

All traits were analysed as single-trait mixed models using Model 1 (M_1), as defined below, as this model was previously proved to be the most appropriate on a smaller data set (Fair *et al.*, 2005). The addition of a further random effect of permanent environment (pe) defined as a unique hen over years was tested for significance for possible inclusion in the model for all single-traits and defined as Model 2 (M_2). Estimates obtained from the most appropriate single-trait analyses were used as starting values in a five-trait analysis. The most appropriate multiple-trait analysis incorporated the "best" models from the single trait analyses and allowed the calculation of relevant correlations among traits together with their respective standard errors.

The two animal models were, Model 1 (M_1) with fixed effects as described above with the three random effects of direct hen (a), temporary environment (te) defined as a unique hen within year and service sire (ss) (the male mate of the breeding pair) and Model 2 (M_2) with a fourth random effect of permanent environment (pe) defined as a unique hen over years.

The mixed models with fixed and random effects are given below in matrix notation:

$$y = X\beta + Z_1a + Z_3te + Z_4ss + e \qquad \ldots\ldots\ldots\ldots\ldots\ldots.. M_1$$

$$y = X\beta + Z_1a + Z_2pe + Z_3te + Z_4ss + e \qquad \ldots\ldots\ldots\ldots\ldots\ldots.. M_2$$

where

y was a vector of phenotypic observations for the five different traits,

X was an incidence matrix relating records to the fixed effects (β);

Z_1, Z_2, Z_3 and Z_4 were incidence matrices relating records to the additive genetic effects (Z_1), permanent environmental effects (Z_2), temporary environmental effects (Z_3) and service sire effects (Z_4),

a, pe, te, ss and e were vectors of additive genetic, permanent environmental, temporary environmental, service sire and residual effects, respectively.

Under an animal model it was assumed that: $Var(a) = A\sigma^2_a$;

where

A is a matrix describing the relationships between animals (i.e., the Numerator Relationship Matrix).

The remaining effects were assumed to be distributed as $Var(pe)= I\sigma^2_{pe}$; $Var(te)= I\sigma^2_{te}$; $Var(ss)= I\sigma^2_{ss}$ and $Var(e)= I\sigma^2_e$ where I = identity matrices of order equal to the number of hen-year combinations (for pe and te), number of service sires and number of records respectively and σ^2_a, σ^2_{pe}, σ^2_{te}, σ^2_{ss}, and σ^2_e direct genetic variance, permanent environmental variance (female over year), temporary environmental variance (female within year), variance due to service sire and environmental (residual) variance respectively.

Convergence was considered to have been obtained when the REML Log-likelihood changed less than 0.002 and the individual variance parameter estimates changed less than 1 % (Gilmour *et al*., 2006). M_1 with random effects tested previously by Fair *et al*. (2005), namely additive genetic, temporary environmental (hen month) and service sire, was run to obtain a log likelihood ratio to compare with that obtained from M_2 containing the additional random effect of permanent environment (hen over year). The re-run of M_1 was necessary due to an increase in the size of the data set initially analysed and the increase in depth of pedigree, thus facilitating the partitioning of the additive and permanent environmental variances. The updated data set was roughly double the size of the previously used data set, and included new data up to the year 2005.

When -2 X the difference between Log-likelihoods for two models being considered were greater than 3.841 the inclusion of the extra random effect (pe) was

considered significant (A Chi-square distribution for $\alpha = 0.05$ with one degree of freedom was used to obtain the critical test statistic of 3.841).

4.3   Results and Discussion

Descriptive statistics for monthly egg and chick production (EP and CP), mean egg and chick weights (MEW and MCW) and hatchability (H) per hen after editing are presented in Table 4.1. Records available for analyses ranged from 13 876 to 7 394 for the five traits. EP and CP had relatively high ranges of 0-17 and 0-16 resulting in the high coefficients of variation (CV) of respectively 93 and 128%. High CV's, albeit somewhat lower than those in the present study, are commonly reported for annual egg and chick production in ostrich females (Deeming, 1996; Van Schalkwyk *et al*., 1996; Bunter *et al*., 2001a; Bunter & Cloete, 2004; Cloete *et al*., 2004). A high frequency of zero records presumably contributed to excessive variation in monthly egg and chick production records. The high maximum of 17 eggs for EP and 16 chicks for CP were not the norm and were achieved only by seven and five hens respectively.

Table 4.1   Descriptive statistics for monthly egg and chick production (EP and CP), mean egg and chick weights (MEW and MCW) and hatchability (H) per hen

Trait	*n*	Mean ± SD	Range	CV (%)
EP	13 876	5.50 ± 5.14	0-17	93
CP	13 876	2.75 ± 3.53	0-16	128
MEW (g)	9 446	1405 ± 142	350-1952	10
MCW (g)	7 394	857 ± 93	505-1249	11
H (%)	9 530	45.8 ± 32.9	0-100	72

n = No of records, SD = standard deviation, CV% = coefficient of variation, EP = total number of eggs per month per hen, CP = total number of live day-old chicks per month per hen, MEW = mean egg weight per month per hen, MCW = mean chick weight of live day-old chicks per month per hen, H = percentage of chicks hatched (EP / CP) x 100

Coefficients of variation of MEW and MCW's were comparatively low (10 and 11% respectively), and are consistent with values for average annual hen records in other studies (Bunter *et al*., 2001a; Cloete *et al*., 2004). Comparing MEW and MCW means show an average weight loss of 39% between setting and hatching.

This loss is desirable as insufficient weight loss results in chicks dying in the shell. Van Schalkwyk *et al*. (2000) reported that the hatchability of artificially incubated ostrich eggs is relatively low and highly variable, ranging, on average, from less than 30% to 60%. This low figure is, according to Brand & Cloete (2006) and Brand *et al*. (2007, 2008), due to shell deaths in approximately 20% of the cases.

The mean of 45.8 ± 32.9% and high CV of 72% for H indicates that just over 54% of eggs laid do not hatch. The low mean H (with a high ± SD) accords with results reported by Bunter (2002), Lambrechts (2004) and Fair *et al*. (2005). Cloete *et al*. (1998) reported a similar hatchability of 47% which was obtained from approximately 23 000 eggs. The range of hatchability (0 to 100%) shows that it is theoretically possible to achieve 100 % hatchability in some cases.
A summary of the analysis of variance for the fixed effects of the five traits are given in Table 4.2. Although the fixed effect of male age for the traits EP and MCW were not significant at the 5% level, the effect did account for some variation and were significant at the 12.1 and 9.6% level respectively (P=0.121 and 0.096). The linear effect of days of production was not significant for MEW and MCW. The effect was, however, left in the model so that all traits could be fitted with the same model in terms of fixed effects to help clarify what the contributions of the different random effects were. All other fixed effects were highly significant (P<0.001) for all traits.

Table 4.2   Model specification for fixed effects for the two quantity and three quality traits studied

Source (fixed effects)	df (range)	EP	CP	MEW	MCW	H
Production days (linear covariate)	1	***	***	ns	ns	***
Contemporary group (CG)	44	***	***	***	***	***
Female age (fage)	6	***	***	***	***	***
Male age	6	ns	*	*	ns	***
Month (MD)	7	***	***	***	***	***
CG x MD	298 - 307	***	***	***	***	***
MD x fage	42 - 44	***	***	***	***	***

df = degrees of freedom, *** P<0.001; * P<0.05; ns = non significant
EP = total number of eggs laid per month per hen
CP = total number of chicks hatched per month per hen
MEW = mean egg weights, total weight of eggs laid per month per hen) / EP
MCW = mean chick weights, total weight of day-old chicks hatched per month per hen) / CP
H = hatch percentage calculated as ((CP/EP) x 100)

All traits were affected by significant interactions between CG and month of production. Although the interactions were examined graphically it was difficult to derive a robust explanation for the cause of such interactions. It is speculated that it may be associated with short-term climate and other micro-environmental factors influencing short-term egg or chick production. With a semi-extensive production system in ostriches, such effects are not as easily controlled as with small domesticated poultry species. The fixed interaction effects were considered as significant nuisance variances and left in the model to increase the accuracy of estimation of the desired parameters; their results (interactions) are thus not presented or discussed in detail.

Figure 4.1   Egg production (EP) according to the month of the breeding season for seven categories of hen age. Vertical lines about the means denote standard errors.

Egg production per month plotted for each category of hen age, averaged over years (15 years from 1991 to 2005), are depicted in Figure 4.1 while chick production per month is shown in Figure 4.2. There was an overall trend for all hen ages, other than 2-year old females, to peak in egg production from August to September (late winter-early spring) followed by a general slump or rest period in October followed by a second lower peak from November to December (mid-summer). This general trend is consistent with that reported by Lambrechts (2004) for hens paired off prior to the winter solstice. Hens reach a maximum monthly egg production at the age of 3 years. These hens produced 7.98 ± 0.32 eggs at the height of the breeding season in

September. Hens in the category of 12 years and older, produced the highest number of eggs after October ending the breeding season with the highest mean egg yield of 4.97 ± 0.39. These older hen's eggs did not produce more chicks than the hens between 4 and 11 years old and were only higher in mean monthly CP than the two- and three-year olds as seen in Figure 4.2.

Two-year old hens produce the least eggs, starting slowly, increasing steadily with a slight slowing down in production in September with highest production in October at 4.56 ± 0.37 eggs. Overall production by the end of the breeding season remained the lowest of all age groups. The 2-year old hens, though producing the least eggs, exhibit a similar downward trend to the older hens in the last three months of the breeding season. Lack of sexual maturity and past experience could be the reason why the young hens start producing later in the breeding season and lay fewer eggs in total than older hens (Jarvis, et al., 1985). The overall mean egg production of 2-year old females for the year was 3.48 ± 0.37 and was consistently below the flock mean annual EP of 5.50 ± 5.14 (Table 4.1).

Three-year old hens were slower to start producing after the commencement of the breeding season compared to the older birds and peak in September to August. They do however produce more than the 2-year old hens and follow the same general trend of the hens of 4 to 12+ years. The 3-year old hens peak in September with a mean EP of 7.98 ± 0.32 which was slightly more in absolute terms (0.33 eggs) than the 8 to11-year old hens which produced a maximum of 7.65 ± 0.31 eggs in August.

The overall trends for CP at the different hen ages were not dissimilar to those found for EP. Inspection of Figure 4.2 suggests three main categories of CP for the hen ages, namely 2, 3-11 and 12+ year old hens.
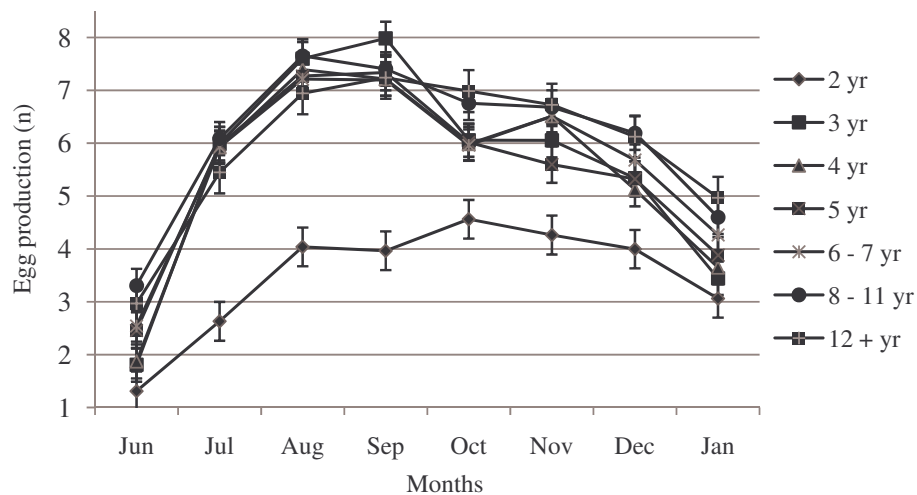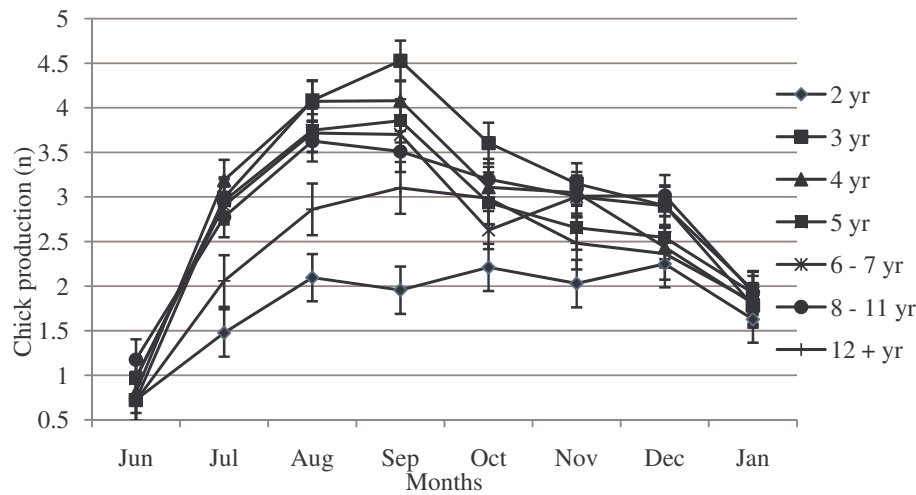
Figure 4.2 Chick production (CP) per month of the breeding season for seven categories of hen age. Vertical lines about the means denote standard errors.

Two-year old hens generally produced fewer eggs and chicks than their older contemporaries except at the commencement and cessation of breeding. The 2-year old hens increase CP steadily up to August remaining around 2 chicks per month reaching their maximum of 2.25 ± 0.26 chicks in December. The 3-year old hens produce more and sooner than the 2-year old hens and follow the general trend of the older hens (4-12+) more closely. CP for hens in the category 3-year olds had the highest peak with a maximum of 4.53 ± 0.23 chicks in September before dropping off steadily to January. The hens that were 3, 4, 5, 6 and 7-years old all peaked in August to September. The mean number of chicks produced for these hens ranged from 3.70 ± 0.22 to 4.53 ± 0.23 per month. The 12-year and older hens decreased in CP more rapidly than other categories, reaching a low of 2.48 ± 0.29 chicks in November, whereas 2-year old hens produced 2.03 ± 0.27 chicks in November. Although 12 year and older hens produced 6.73 ± 0.40 eggs in November (Figure 4.1) the viability of these eggs seemed compromised as seen from the low number of chicks produced (Figure 4.2).
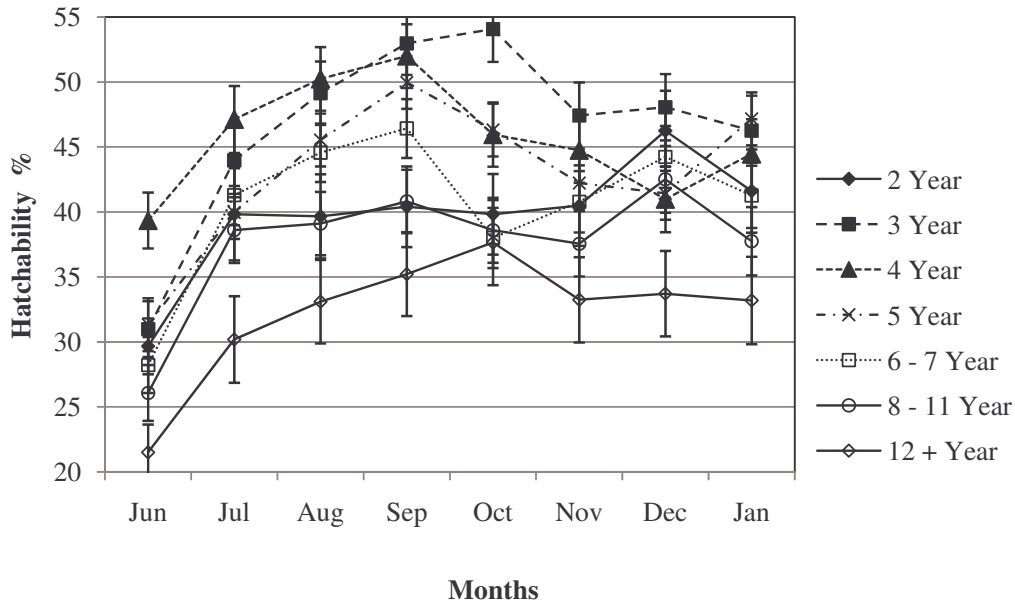
Figure 4.3   Hatchability per month of the breeding season for seven categories of hen age. Vertical lines about the means denote standard errors.

The mean H for the population was 45.8% (Table 4.1) whereas the 12 year and older hen category had a reduced overall H of 39%. The mean H for the category 3 year hens was 49%. All categories of hen ages decrease sharply from December to January. Hatchability is shown in Figure 4.3 for the seven age categories of hen age.

It is clear from Figure 4.3 that H is overall the highest for 3 year old hens 54.07 ± 2.52% and steadily decreased as the hens' age increases. Overall means for H of 3, 4, 5 and 6-7 year olds for the season were 46.61 ± 2.49, 45.61 ± 2.48, 43.00 ± 2.58 and 40.60 ± 2.32%, respectively. Two-year old hens that produced overall the least number of eggs however had a higher overall mean H of 39.72 ± 3.06% than 8 – 11 and 12+ year olds with overall means of respectively 37.63 ± 2.47 and 32.23 ± 3.14%. These differences are not significant when comparing overlapping standard errors. Twelve+ year old hens had the lowest H throughout the breeding season indicating that although older birds do not produce the least number of eggs or the least number of chicks, they do produce the lowest percentage of viable eggs as also reported by Bunter (2002).

The qualitative trait of MEW per month of the breeding season for seven categories of hen age is shown in Figure 4.4. Two- and 12 + year-old hens produced

lower mean egg weights than the other age categories throughout the breeding season.   Mean egg weights ranged from 1396 ± 11 to 1444 ± 11 g from August to January for 3, 4, 5 and 6-7 year old hens all staying relatively constant throughout the season. The highest mean egg weight 1444 ± 11 g for 4-year-old hens occurred in November with the lowest 1294 ± 14 g for 2-year-olds in July. These mean egg weights are in accordance with those of 1416 ± 128 g, 1419 ± 123 g and 1425 ± 107 g reported by Bunter *et al.* (2001a), Cloete *et al.* (2004) and Brand *et al.* (2008) respectively.

The mean chick weights followed similar trends to that of the mean egg weights and thus will not be graphically presented. The MCW for the category 3, 4, 5 and 6 – 7-year-olds lie in a narrow range (13.58 g) from 865 ± 8 to 879 ± 8 g for the months September to January. The lowest absolute value of 819 ± 10 g MCW was for 12+ year-olds in June and the highest absolute of 865 ± 8 g MCW for 5-year-olds in October. The low mean egg and chick weight for 12 + year old hens could in part be associated with the H (Figure 4.3) being the lowest for this hen age category.
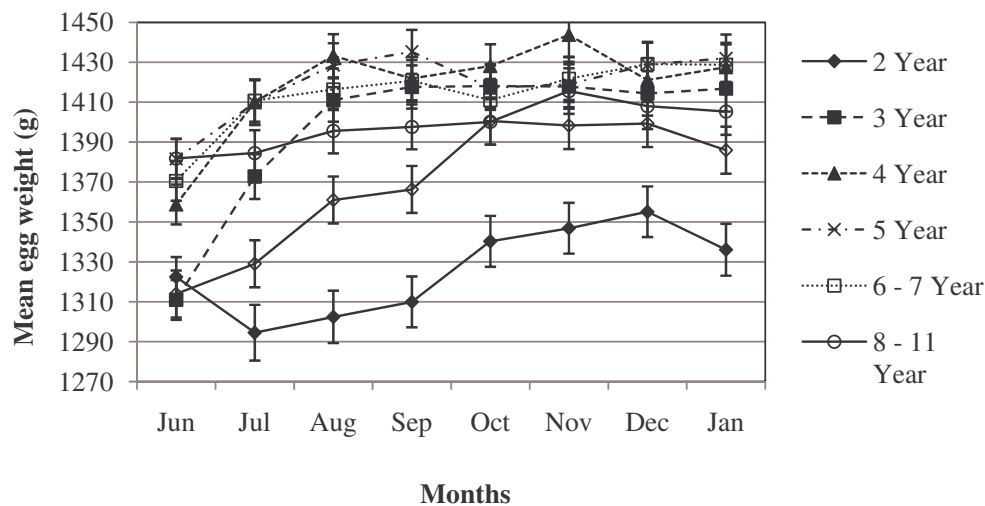

Figure 4.4   Mean egg weight (MEW) per month of the breeding season for seven categories of hen age. Vertical lines about the means denote standard errors.

Model selection pertaining to the random part was done according to Log-likelihoods. Log-likelihoods obtained for each trait under the two different models

(inclusion or exclusion of the permanent environmental effect) with the most appropriate model in bold, are given in Table 4.3.

Model 1 with three random effects tested previously by Fair *et al*. (2005), namely additive genetic, temporary environmental (hen month) and service sire, was consistently inferior to Model 2, containing the additional random effect of permanent environment (PE) (hen over year), for all traits except for MCW.

Table 4.3 Log-likelihoods and differences obtained for two models (M_1) and (M_2) fitted for the traits EP, CP, MEW, MCW and H

Model	EP	CP	MEW	MCW	H
Model 1	-6 099.01	-1 550.41	-6 274.88	-2 152.05	-5 362.17
Model 2	-6 095.22	-1 544.27	-6 271.16	-2 152.05	-5 353.93
Difference	-3.79	-6.14	-3.72	0.00	-8.24
-2 x Difference	**7.58**	**12.28**	**7.44**	0.00	**16.48**

Difference = Log-likelihood differences after inclusion of the random effect pe; EP = total number of eggs per month per hen; CP = total number of live day old chicks per month per hen; MEW = mean egg weight per month per hen; MCW = mean chick weight of live day-old chicks per month per hen; H = percentage of chicks hatched (EP / CP) x 100

Estimated variance components and ratios (± s.e.) and of correlations among EP, CP, MEW, MCW and H, as derived from five-trait analyses are presented in Table 4.4. Although estimates differ in the literature (Bunter *et al*., 2001*a;* Cloete *et al*., 2004; Lambrechts, 2004; Cloete *et al*., 2005; Fair *et al.*, 2005; Brand *et al*., 2008; Cloete *et al.,* 2008b), it must be born in mind that models and size of data were not the same. Moreover, the models used in this study were fitted to monthly records across years, resulting in medium sized data sets (larger than previously used) with the potential of greater parameterization of the fixed and random effects being analysed. The fact that analyses of the larger data sets were possible was mainly due to the general improvement of computer software and hardware.

Derived heritability (h^2) estimates for the reproduction traits (EP, CP and H) were low, ranging from 0.02 to 0.05 (Table 4.4). The quality traits (MEW and MCW) were highly heritable at respectively 0.44 and 0.67.

Table 4.4 Heritability estimates (h^2), permanent and temporary environmental and service sire variance ratios (c^2_{pe}, c^2_{te}; c^2_{ss}) and genetic, permanent and temporary environmental and service sire correlations among different traits as derived from five-trait analyses with phenotypic variance in brackets on the diagonal

Traits	EP	CP	MEW	MCW	H
Additive genetic correlations (h^2 in bold)					
EP	**0.04 ± 0.02** (20.0)	1.00 ± 0.05	-0.03 ± 0.20	-0.05 ± 0.15	0.98 ± 0.29
CP		**0.05 ± 0.03** (10.6)	0.10 ± 0.17	0.11 ± 0.13	0.95 ± 0.14
MEW			**0.44 ± 0.04** (20442)	0.94 ± 0.03	0.52 ± 0.27
MCW				**0.67 ± 0.02** (11322)	0.47 ± 0.25
H					**0.02 ± 0.02** (822)
Permanent environmental correlations (c^2_{pe} in bold)					
EP	**0.08 ± 0.03**	0.76 ± 0.08	0.34 ± 0.19	-	0.33 ± 0.16
CP		**0.08 ± 0.03**	0.27 ± 0.19	-	0.81 ± 0.07
MEW			**0.09 ± 0.02**	-	-0.01 ± 0.18
MCW				**-**	-
H					**0.11 ± 0.02**
Temporary environmental correlations (c^2_{te} in bold)					
EP	**0.15 ± 0.01**	0.74 ± 0.02	0.48 ± 0.04	0.35 ± 0.05	0.36 ± 0.04
CP		**0.16 ± 0.01**	0.40 ± 0.04	0.37 ± 0.05	0.85 ± 0.02
MEW			**0.13 ± 0.01**	0.87 ± 0.02	0.31 ± 0.04
MCW				**0.07 ± 0.01**	0.33 ± 0.05
H					**0.15 ± 0.01**
Service sire correlations (c^2_{ss} in bold)					
EP	**0.05 ± 0.01**	0.79 ± 0.06	0.28 ± 0.18	0.04 ± 0.19	0.37 ± 0.16
CP		**0.06 ± 0.01**	0.11 ± 0.18	-0.08 ± 0.19	0.82 ± 0.06
MEW			**0.04 ± 0.01**	0.97 ± 0.05	-0.15 ± 0.21
MCW				**0.04 ± 0.01**	-0.31 ± 0.11
H					**0.05 ± 0.01**

EP = total number of eggs per month per hen; CP = total number of live day-old chicks per month per hen; MEW = mean egg weight per month per hen; MCW = mean chick weight of live day-old chicks per month per hen; H = percentage of chicks hatched (EP / CP) x 100

The only previous study where h² was estimated for monthly egg production was that of Lambrechts (2004) where a direct genetic variance ratio (h^2) of 0.08 and a dam permanent environmental variance ratio (c^2_{pe}) of 0.07 for egg production

potential in a sample of birds from the same resource flock were reported. The summation of these ratios (h^2 and c^2_{pe}) amount to 0.15, which is not too dissimilar to the corresponding estimate of 0.12 found in the present study, where the models fitted differed and the dataset was larger and more informative because it included more recent data and a greater proportion of familial links in the flock. The present h^2 estimates are lower than those estimated for annual EP (0.12 ± 0.11) and CP (0.11 ± 0.11) by Bunter *et al*. (2001a). These estimates are also lower than corresponding estimates of respectively 0.26 and 0.21 subsequently estimated for annual EP and CP by Cloete *et al*. (2004), using a larger and more informative data set. Being fewer hen-year records, the model used by the mentioned authors, did however not include the random effect of TE.

The estimates for MEW and MCW were in correspondence with respective initial h^2_a estimates of 0.43 and 0.51 reported by Bunter *et al*. (2001a). Corresponding estimates reported by Cloete *et al*. (2004) were higher, at 0.72 and 0.74. It is reasonable to assume that h^2 estimates derived from data accrued over an entire breeding season would exceed those derived from within season analyses, since the latter data were found to be inherently more variable (see Table 4.1 and the corresponding discussion).

Estimates for PE (c^2_{pe}) were fairly consistent, ranging from 0.08 for EP and CP to 0.09 and 0.11 for MEW and H respectively. This is lower than values found by Cloete *et al*. (2008b), which ranged from 0.17 to 0.19 for EP and CP. These models did not include the TE effect which could account for the difference between the sets of values. Estimates were also lower than those found by Brand *et al*. (2008) (MEW-0.32) and Cloete *et al*. (2006) (H-0.21) again model differences being the most likely explanation of difference in partitioning of the effects.

Corresponding estimates for TE were fairly constant, ranging from 0.07 for MCW to 0.16 for CP. This is in accordance with values found by Fair *et al*. (2005), which ranged from 0.09 for MCW to 0.18 for H. The only previous TE estimates found in the literature was an estimate of 0.13 for EP in the study of Lambrechts (2004). This estimate is in good agreement with the corresponding estimate of 0.16 in the present study.

Service sire effects were significant for all traits, but failed to exceed 6 % of the overall phenotypic variance (Table 4.4). Previous estimates of service sire variances were generally not significant for EP, but in the same range for CP (0.11 -

Bunter *et al*., 2001a; 0.09 - Cloete *et al*., 2004; 0.10 - Cloete *et al.,* 2008b). The service sire variance ratio for MEW amounted to 0.04 in the present study, which accords with a previous estimate of 0.08 although somewhat lower (Cloete *et al.,* 2004). The present estimate for MCW (0.06) corresponds well to previous estimates in the literature (0.06 - Bunter *et al.,* 2001a; 0.07 - Cloete *et al.,* 2004).

The correlation of monthly EP and CP were unity on a genetic level (Table 4.4). Previous estimates of animal genetic correlations between EP and CP were correspondingly high at 0.86 (Bunter *et al*., 2001b), while it exceeded the theoretical limit of unity in the studies of Cloete *et al*. (2004) and Lambrechts (2004). These traits can thus be considered as effectively the same, when assessed on the level of the individual female. Egg production and CP were favourably correlated with H on a genetic level (0.98 ± 0.29 and 0.95 ± 0.14 respectively). Previous estimates in the literature also suggested that EP and H were favourably correlated on the genetic level (Lambrechts, 2004). The favourable genetic correlation of CP with H was expected, since an increased H would result in a higher CP.

Between animal genetic correlations of EP with respectively MEW and MCW amounted to 0.22 and 0.05 (Bunter *et al*., 2001b). It should be born in mind that Bunter *et al.* (2001b) did not partition h^2 and c^2_{te} i.e. both were pooled in a single animal effect. Corresponding correlations of CP with MEW and MCW were 0.28 and 0.23 respectively. In the literature, respective genetic correlations of EP with MEW and MCW were 0.26 and 0.00 (Cloete *et al.,* 2004). Corresponding correlations of CP with MEW and MCW were 0.27 and 0.14 respectively. Genetic correlations of EP and/or CP with MEW and/or MCW that are antagonistic in sign may not be entirely unexpected, since such relationships are often found in poultry (Bunter, 2002). However, this study supported evidence that MEW and MCW were not unfavourably related to CP in ostriches, thus simplifying decisions regarding a practical selection index based on economic principles. The production of chicks is the primary objective in ostrich breeding. Low live weight chicks at day-old were more likely to succumb in the month following artificial hatching than their heavier contemporaries (Cloete *et al.,* 2001). Unfavourable genetic correlations of CP with MEW and MCW thus would have the potential to impair the viability of chicks in commercial operations. The genetic correlations of H with MEW with MCW were positive (0.52 and 0.47 respectively), indicating no antagonistic relationship. As expected, the genetic correlation of MEW and MCW was very high at 0.94, as it was

also found by Bunter *et al.* (2001b - 0.91) and Cloete *et al.* (2004 - 0.88). These results suggest that selection for improved reproduction in ostriches is possible. Selection for reproduction is furthermore unlikely to be complicated by unfavourable correlations with H, MEW and MCW.

Permanent-, temporary environmental and service sire correlations generally followed genetic correlations in sign and magnitude (Table 4.4). Exceptions were permanent, temporary environmental and service sire correlations of EP with MEW and MCW, which were generally positive in sign and larger in magnitude. These results suggest that an environment favouring increased levels of reproduction would also benefit average egg and chick weights. The service sire correlation of the number of infertile eggs with CP amounted to 0.68 in the study of Bunter *et al.* (2001b).

The corresponding correlation between CP and H in the present study was 0.82 ± 0.06. Service sire correlations of MEW and MCW with H were -0.15 ± 0.21 and -0.31 ± 0.11, which was generally lower than the corresponding genetic correlation, and different in sign. The service sire correlation for number of infertile eggs produced by females and average chick weight were negative at -0.08 ± 0.19, but not significant given the SE. It thus seems that characteristics inherent to service sires as far as egg and chick weights are concerned, are not related to those characteristics determining the hatchability of eggs produced by their mates.

4.4   Conclusions

This study reported age specific seasonal production patterns for ostrich females indicating that seasonal production trends of 2-year-old females differed from those of older females. Ostrich breeding is characterized by relatively few parents producing substantial numbers of full sib offspring. Potential candidates for selection can well be assessed for reproduction based on own performance and not only on maternal performance, as was the case thus far (Cloete *et al*., 2004). Hens in the age group categories of 3, 4, 5 and 6 - 7 years old outperformed 2 and 12+ year olds for the quantitative (CP and H) and qualitative (MEW and MCW) traits. Superior young hens should be identified and selected for replacement while hens

that are 12+ years old should be replaced. Three-year olds produced the highest mean number of chicks suggesting selection decisions on own performance could possibly be taken at this stage. According to heritabilities estimated all reproduction traits analysed would respond to heightened selection pressure. There was no evidence of serious unfavourable correlations between quantitative and qualitative traits in ostrich females, thus supporting previous findings to this effect.

5

EXPLORING THE USE OF RANDOM REGRESSION MODELS FOR MODELLING ANIMAL EFFECTS ON EGG AND CHICK PRODUCTION TRAITS OF OSTRICH FEMALES OVER YEARS

5.1   Introduction

Guidelines for selection to improve egg production (EP) and chick production (CP) in the commercial ostrich industry should be based on knowledge of genetic and non-genetic influences on the economically important production traits of interest. Improved EP and CP would be of little use if quality traits such as mean egg weight (MEW), mean chick weight (MCW) and hatchability% (H) were not enhanced or optimised, or at the very least maintained at the same level. H is of obvious importance in enhancing chick output, while chick weight is commonly used for the grading of ostrich chicks (Verwoerd *et al.,* 1999).

Selection for improved egg production should thus be based on these quality as well as quantity traits. Early identification of superior animals that maintain high levels of production over their lifetime is desirable. Studies are thus required to investigate the relationships between repeated cycles of reproduction over years, to ascertain whether adequate genetic variation for accurate selection is present early in the productive life of the animals.

At this stage, it is unknown whether the heritability of repeated performance traits of ostrich females across subsequent production seasons changes with age. Typical ostrich flocks have a relatively slow turnover, leading to relatively few replacements being selected annually (Cloete *et al.,* 1998). It is thus not practical to set up multi-trait analyses with production at different ages being treated as independent traits for establishing age-trends in the heritability of these traits. This study therefore focuses on exploring the use of random regression models to model production over years as an alternative. Random regression models to analyse longitudinal or repeated measures data has become common practice amongst animal

breeders (Schaeffer, 2004; Tier & Meyer, 2004; Buxadera & da Mota, 2008; Wolc, *et al.,* 2009).

The availability of pedigree and census data collected over several years meant an animal model using mixed model methodologies could be fitted while simultaneously considering the longitudinal nature of hen production traits over time by combining it with a random regression model. The quantity and related quality traits were analysed to investigate the consistency of genetic and non-genetic parameters over time, using random regression methodology.

5.2   Material and Methods

Data of pedigree and performance for 80 943 individual egg and chick records were obtained from a large pair breeding flock maintained at the Oudtshoorn Research Farm in South Africa. The data were collected from 1991 to 2005 and the eggs/chicks produced were the progeny of 540 females and 530 males that were pair-mated to comprise 654 unique breeding pairs. All breeding pairs were kept in separate breeding paddocks to facilitate ancestry identification of the offspring. Weights of laid eggs and hatched day-old chicks, parent details and date of lay of eggs were recorded. Eggs were collected daily. The general management of the breeding pairs and the eggs has been described in detail (Van Schalkwyk *et al.,* 1996; Cloete *et al.,* 1998; Bunter, 2002).

The traits analysed were treated as traits of the hen: The traits considered were the two quantity traits of egg production (EP), defined as the total number of eggs laid per hen per year and chick production (CP), defined as the total number of chicks hatched per hen per year. The three quality traits were mean egg and chick weights (respectively MEW and MCW) per hen per year and hatch percentage (H). Hatch percentage was calculated as CP/EP x 100 per year per hen. The 80 943 individual records were edited to form 2 460 unique hen by year records.

The ages of the individual hens and sires were known and ranged from 2 to 21 years for hens and 2 to 21 years for sires (*fage* and *mage*), year of egg production (1991 to 2005) was combined with some nutritional experimental groups, as well as some ostrich genotypes (Zimbabwe Blues and South African Blacks) to form 62 contemporary groups (CG), these effects were analysed for inclusion in the model if

significant. The number of production days was also included as a linear covariate for EP, CP and MEW as not all hens had equal number of days to breed due to random deaths of male and female birds throughout the breeding season.

ASREML (Gilmour *et al.*, 2006) was used to estimate variance components. The software allows for the estimation of various random effects under an animal model, and also predicts least squares means for selected fixed effects. Fixed effects were tested at the $\alpha = 0.05$ level with numerator degrees of freedom (df) of (n-1) where n was the number of levels of each fixed effect and denominator df as given by ASREML for the residual variance. The testing of fixed effects for inclusion in the model was repeated for each of the five traits analysed.

The traits were analysed by fitting single-trait animal models with random regressions fitted either as intercept only, or intercept with linear or quadratic polynomials. Fixed effects included in analyses were as described above while the four random effects fitted were direct genetic additive (a) and permanent environment (pe) effects (as a random regression with intercept and linear or quadratic polynomial for age of hen (fage)) and, service sire (ss) (the male mate of the breeding pair) and breeding paddock (bp).

The effect of male age was fitted as a random cubic spline (spl) term, the random component modelling deviations from a fixed linear trend (lin) conforming to a smoothed trend for male or female age. Random lack-of-fit deviations from linearity not associated with a smooth trend were also modelled initially. The distribution of fage x mage effects was such that it became impossible to model this interaction as fixed sources of variation in initial analyses, as many cells in such an interaction table would be empty or near empty. Lin(fage).lin(mage) and also random spl(fage).spl(mage) were tested for inclusion in the model.

The initial mixed model employed was as follows:

$$y_{ijklmno(t)} = \mu + b_j(Production - days)_j + cg_k + b_l(fa_l) + b_m(ma_m) + (fa_l \; x \; ma_m) + \sum_{h=1}^{m-1} ma_m S_{hm}$$

$$+ \sum_{g=1}^{f-1} fa_f S_{gf} + \sum_{n=0}^{n_g} u_{io} \emptyset_n + \sum_{n=0}^{n_c} pe_{io} \emptyset_n + ss + bp + e_{ijklmno}$$

where:

$y_{ijklmno(t)}$ was a vector of phenotypic records for the five traits EP, CP, MEW, MCW and H respectively, for hen i (for i = 1,...,n), recorded at the tth age of

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the hen (for t = 2,...,20); b_j was the linear regression coefficient for the co-variable effect of days of production available per hen; cg_k , fixed effect of contemporary group (for k = 1,...,62); b_l the linear regression coefficient for female age l (for l = 2,...,11); b_m the linear regression coefficient for male age m (for m = 2,...,21); and the female by male age interaction; S were splines fitted with h and g knots for male age (ma_m) and female age (fa_f) respectively; u_{io} and pe_{io} are the oth random regression coefficients for additive and permanent environmental effects, respectively, for hen i; $\emptyset_{itn}$ was the nth polynomial for the record of hen i at age t; n_g and n_c was the order of the polynomial fitted for additive and permanent environmental effects; ss and bp were the random effects of service sire (the mate of the hen i) and breeding paddock of the breeding pair, respectively; μ was the overall mean of the data and $e_{ijklmno}$ was the random residual.

The model is given below in matrix notation:

$$y = Xb + Z_1a + Z_2pe + Z_3ss + Z_4hp + e \qquad \text{……………………..} \; M_1$$

where:

y was a vector of phenotypic observations for each of the five traits analysed (EP, CP, MEW, MCW and H),

X was an incidence matrix relating records to the fixed effects,

b was a vector of solutions for the fixed effects and

Z_1 and Z_2, were covariance matrices for additive genetic effects (Z_1) and permanent environmental effects (Z_2). It was assumed that var(a) = A$\otimes$G, var(pe) = I$\otimes$PE, where A is the numerator relationship matrix, $\otimes$ is the Kronecker product (direct product) and G and PE are of the order of polynomial fitted for a and pe effects respectively. Z_3 and Z_4 were incidence matrices relating records to service sire effects (Z_3) and breeding paddocks (Z_4) where Var(ss)= $I\sigma^2_{ss}$, Var(bp)= $I\sigma^2_{bp}$, and I = identity matrices of order equal to the number of service sires and number of breeding paddocks respectively and Var(e)= $I\sigma^2_e$ = R where σ^2_{ss}, σ^2_{bp}, and σ^2_e were variances due to service sire, breeding paddock and environmental (residual) respectively. Where a and pe were vectors of random regressions coefficients for animal

additive genetic and permanent environmental effects and bp, ss and e were vectors of service sire, breeding paddock and residual effects, respectively.

The mixed model equations (MME) in matrix notation were:

$$\begin{pmatrix} X'R^{-1}X & X'R^{-1}Z_1 & X'R^{-1}Z_2 & X'R^{-1}Z_3 & X'R^{-1}Z_4 \\ Z_1'R^{-1}X & Z_1'R^{-1}Z_1 + A^{-1} \otimes G^{-1} & Z_1'R^{-1}Z_2 & Z_1'R^{-1}Z_3 & Z_1'R^{-1}Z_4 \\ Z_2'R^{-1}X & Z_2'R^{-1}Z_1 & Z_2'R^{-1}Z_2 + I \otimes P^{-1} & Z_2'R^{-1}Z_3 & Z_2'R^{-1}Z_4 \\ Z_3'R^{-1}X & Z_3'R^{-1}Z_1 & Z_3'R^{-1}Z_2 & Z_3'R^{-1}Z_3 + \sigma_{ss}^{-2}I & Z_3'R^{-1}Z_4 \\ Z_4'R^{-1}X & Z_4'R^{-1}Z_1 & Z_4'R^{-1}Z_2 & Z_4'R^{-1}Z_3 & Z_4'R^{-1}Z_4 + \sigma_{bp}^{-2}I \end{pmatrix} X \begin{pmatrix} \hat{b} \\ \hat{a} \\ \widehat{pe} \\ \hat{ss} \\ \widehat{hp} \end{pmatrix} = \begin{pmatrix} X'R^{-1}y \\ Z_1'R^{-1}y \\ Z_2'R^{-1}y \\ Z_3'R^{-1}y \\ Z_4'R^{-1}y \end{pmatrix}$$

The four random effects a, pe, ss, and bp were tested by adding them to the fixed model in a stepwise approach to determine the "best model" based on the Log-likelihood (LL) ratio test (-2 x the difference between LL obtained from consecutive models given the addition of one random effect is considered significant when > 2.71, ASREML Users Guide 3, page 17,). The critical value of 2.71 rather than 3.84 for testing the inclusion of an additional effect is a one sided test.

Convergence was attained when the changed less than 0.002 and the individual variance parameter estimates changed less than 1% (Gilmour *et al.*, 2006).

Polynomial random regressions with intercept and/or linear and/or quadratic slopes fitted to the additive and permanent environmental effects were then tested for significance in a similar fashion.

The results of the analyses of the random regression models were used to calculate genetic parameters, considering the longitudinal nature of egg production, and thus plot direct heritability and permanent environmental variance ratios to determine when selection decisions on own performance could be taken.

5.3   Results and Discussion

Descriptive statistics for yearly total production traits EP, CP, MEW, MCW and H are presented in Table 5.1. There were 2 460 hen by year records available for analyses derived from 80 943 egg and chick weight records.

Table 5.1   Descriptive statistics for the production traits EP, CP, MEW, MCW and H from the 2 460 hen by year records after editing

Traits	Number of records with a zero for the trait	*n*	Mean ± SD	Range	CV (%)
EP	110	1 822	42.9 ± 25.34	0 - 121	59
CP	288	1 822	21.1 ± 17.7	0 - 90	84
MEW (g)	-	1 705	1 411.0 ± 126.5	825 - 3 315	9
MCW (g)	-	1 548	856.6 ± 82.8	607 - 1 517	10
H	178	1 712	45.4 ± 24.9	0 - 100	55

n = number of records available for appropriate model given the particular trait after editing, SD = standard deviation, CV% = coefficients of variation; EP = mean total number of eggs per year; CP = mean total number of chicks per year; MEW = mean egg weight per year; MCW = mean chick weight per year and H = % hatched per hen per year.

The numbers of records available for analyses after editing the data were 2 460 for the five traits. EP, CP and H had 110, 288, and 178 records respectively equal to zero comprising of 6, 16 and 10% of the data. Although the number of records for the five traits is considered comparatively small by animal breeders' standards, it must be remembered that no other ostrich data with pedigree records were available and that these numbers represent 80 943 individual egg and chick weight records collected over a period of 15 years. Coefficients of variation for EP and CP (59 and 84%) were high due mainly to their wide ranges of production, 0-120 and 0-90 respectively. These high values are consistent with previously reported studies in ostriches (Deeming, 1996; Van Schalkwyk *et al.,* 1996; Bunter *et al.*, 2001a; Cloete *et al.*, 2004; Cloete *et al.*, 2005; Cloete *et al.*, 2008b, Fair *et al.*, 2011).

MEW and MCW have comparatively low coefficients of variation of 9 and 10% respectively, and are partly due to indirect natural and artificial selection for optimal weight ranges to ensure survivability of the chicks Brand *et al.* (2008). Low coefficients of variation that accord with this study were reported by Cloete *et al.* (2008b).

The low mean H of 45.44 ± 24.9 is not uncommon for artificially incubated eggs in the ostrich industry and is similar to results in the literature (Bunter, 2002; Lambrechts, 2004; Fair *et al.*, 2005; Cloete *et al.*, 2005; Cloete *et al.*, 2006). This low H results in financial and genetic losses due to fewer chicks being available for sale and/or selection as replacements.

Mean number of eggs and chicks produced per year per hen age as well as total number of hens per year of hen age are shown in Figure 5.1 for the data before edits.
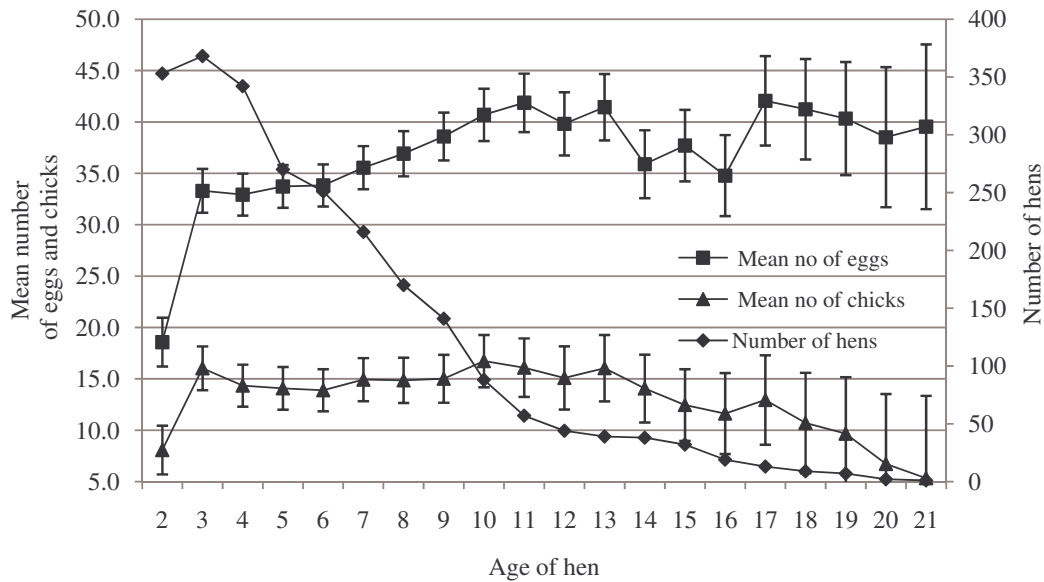

Figure 5.1   Mean number of eggs and chicks produced and total number of hens per year of hen age. Vertical lines about the means denote standard errors.

Mean number of eggs and chicks produced per hen age increased sharply from 18 to 33 eggs and from 6 to 16 chicks per year for two to three-year-old hens. EP then increased steadily up to 42 eggs per year for 11-year-olds whereas CP stayed more constant (between 13 and 16) for 3-year-old hens up to 13-year-old. Increased EP at later ages did not lead to an increased CP, suggesting that H % is compromised in older hens. Embryonic deaths are generally high in artificially incubated ostrich eggs and can be attributed to various causes e.g. female age (mortality increases the older the hen gets), storage time before setting in incubator (eggs set directly and stored for >6 days heightens mortality) and incubator differences to mention a few (Brand *et al.,* 2007).

After 11 years of age the hens' EP decreased to around 40 eggs per year (Figure 5.1). The number of hens per hen age group peaks at 368 hens for 3-year-olds, and then drops steadily to 57 hens that were 11 years of age. Although few birds were 12 to 21 years old they did maintain a relatively high number of mean eggs per year.

The mean number of chicks declined steadily from 16.7 for 10-year-old to 5.3 for 21-year-old hens. Fitting a linear regression for mean CP per year (response variable) and age of hen (independent variable) for 10- to 21-year-old hens, results in a negative gradient of -0.974 (P<0.0001). This translates to roughly one less chick produced per year of age increase for hens older than 10-years of age ($R^2 = 0.91$).

5.3.1 Fixed effects

The fixed effects of days (number of *production days fitted* as a linear co-variate), CG (contemporary groups), female age (fage) were tested for significance using ASREML for possible inclusion in the model. The effect of male age (*mage*) was fitted as a cubic spline. The results for the analyses of the fixed effects for the five traits are shown in Table 5.2.

Table 5.2 Model specification for fixed effects for the two quantity and three quality traits studied

Source (fixed effects)	df (range)	Quantity traits		Quality traits		
		EP	CP	MEW	MCW	H
Days (Linear co variable)	1	***	***	***	ns	ns
Contemporary group (CG)	61	***	***	***	***	***
Female age	9	***	***	***	***	***
Male age	19	ns	ns	ns	ns	ns
Linear male age	1	ns	ns	*	ns	ns
Female x Male age	1	ns	ns	ns	ns	ns
Spline male age	48	*	*	*	ns	*

df = degrees of freedom, *** P<0.001; * P<0.05; ns = non significant
EP = total number of eggs laid per hen per year and chick production
CP = total number of chicks hatched per hen per year
MEW = mean egg weights per hen per year
MCW = mean chick weights per hen per year
H = hatch percentage calculated as ((CP/EP) x 100) per year per hen

Number of production days was not significant for MCW and H although significant for the remaining three traits. Contemporary group (CG) and female age were significant (P<0.001) for all traits (Table 5.2). The effects of linear female and

male age were not significant for all traits except for MEW that was significant (P<0.05) for linear male age. The effects of fitting random splines for female age were all not significant whereas spline male age was significant for all traits except MCW. Although splines are random effects they were used for modelling environmental variation and therefore were tested for inclusion in the model prior to adding the random genetic and permanent environmental effect.

5.3.2   Random effects

Models with LL-values for each of the five traits are presented in Tables 5.3 to 5.7. Model 1 included the fixed effects of days, cg (contemporary groups) and fage (female age). Not all models are shown for the sake of brevity and model comparisons are indicated in the following tables under the column heading "Models compared" e.g. 2 vs. 1, thus -2 x LL differences between Models 2 and 1 was considered a significant difference as 102.74 far exceeds 2.71, signifying that the addition of breeding paddock as a random environmental effect makes a significant contribution to the improvement of the model. Models were only compared on the basis of the addition of a single random effect or adding a linear effect to an intercept, or a quadratic effect to a linear effect.

Results pertaining to LL-values for EP are presented in Table 5.3. Given these results, it was determined that Model 11 was the "best model" for analysing EP.

Table 5.3   Random regression mixed models with Log-likelihoods for egg production with the "best model" in bold

Model	Log-likelihood	-2 x LL Difference for models compared	Models compared	Residual	a	pe	bp	ss
1(fixed effects)	-6 404.71			485	-	-	-	-
2	-6 353.34	102.74	2 vs. 1	418	-	-	√	-
3	-6 305.42	198.58	3 vs. 1	346	-	-	-	√
4	-6 290.27	30.30	4 vs. 3	328	-	-	√	√
5	-6 251.13	78.28	5 vs. 4	295	√0	-	√	√
6	-6 256.56	67.42	6 vs. 4	294	-	√0	√	√
7	-6 247.92	6.42	7 vs. 5	292	√0	√0	√	√
8	-6 221.31	53.22	8 vs. 7	258	√0	√1	√	√
9	-6 229.32	37.2	9 vs. 7	259	√1	√0	√	√
10	singular			-	√1	√1	√	√
11	**-6 215.45**	11.72	**11 vs. 8**	**250**	**√0**	**√2**	√	√
12	-6 223.35	11.94	12 vs. 9	250	√2	√0	√	√

a = direct genetic effect   0 = intercept fitted   √ = included in model
pe = permanent environment   1 = 0 + linear slope fitted   - = not included in model
bp = breeding paddock   2 = 1 + quadratic slope fitted
ss = service sire

Model 11 included the following effects: days (linear co-variable), contemporary group (CG), female age (fage); spline of male age and male age(mage), and direct additive genetic effects (a), animal permanent environmental effects (pe), service sire effects (ss), and breeding paddock (bp), with the intercept fitted for a and a quadratic polynomial random regression for pe. Residual variances are also indicated in Tables 5.3 to 5.7 and generally decreased (as expected) with the inclusion of additional significant effects. A similar situation was seen for CP, MEW, MCW and H.

Table 5.4   Random regression models with Log-likelihoods for chick production with the "best model" in bold.

Model	Log-likelihood	-2 x LL Difference for models compared	Models compared	Residual	a	pe	bp	ss
1	-5 895.50			272	-	-	-	-
2	-5 837.63	115.74	2 vs. 1	231	-	-	√	-
3	-5 767.21	256.58	3 vs. 1	182	-	-	-	√
4	-5 757.28	19.86	4 vs. 3	175	-	-	√	√
5	-5 725.64	63.28	5 vs. 4	160	√0	-	√	√
6	-5 728.04	58.48	6 vs. 4	159	-	√0	√	√
7	-5 722.27	6.74	7 vs. 5	159	√0	√0	√	√
8	-5 691.49	61.56	8 vs. 7	139	√0	√1	√	√
9	-5 696.86	50.82	9 vs. 7	140	√1	√0	√	√
10	singular				√1	√1	√	√
11	**-5 688.47**	6.04	**11 vs. 8**	**135**	**√0**	**√2**	√	√
12	-5 693.64	6.44	12 vs. 9	135	√2	√0	√	√

a =   direct additive genetic effect   0 = intercept fitted   √ = included in model
pe = permanent environment   1 = 0 + linear slope fitted   - = not in model
bp = breeding paddock   2 = 1 + quadratic slope fitted
ss = service sire

Table 5.5   Random regression models with Log-likelihoods for mean egg weight production with the "best model" in bold

Model	Log-likelihood	-2 x LL Difference for models compared	Models compared	Residual	a	pe	bp	ss
1	-8 607.89			12 129	-	-	-	-
2	-8 507.28	201.22	2 vs. 1	9 512	-	-	√	-
3	-8 271.00	673.78	3 vs. 1	5 262	-	-	-	√
4	-8 246.54	48.92	4 vs. 3	4 821	-	-	√	√
5	-7 997.97	497.14	5 vs. 4	3 054	√0	-	√	√
6	-8 003.35	486.38	6 vs. 4	3 068	-	√0	√	√
7	-7 991.11	13.72	7 vs. 5	3 065	√0	√0	√	√
8	-7 953.36	75.5	8 vs. 7	2 439	√0	√1	√	√
9	-7 960.62	60.98	9 vs. 7	2 435	√1	√0	√	√
10	Singular				√1	√1	√	√
11	**-7 923.78**	**59.16**	**11 vs. 8**	**2 063**	**√0**	**√2**	**√**	**√**
12	-7 929.31	62.62	12 vs. 9	2 049	√2	√0	√	√

a =   direct additive genetic effect   0 = intercept fitted   √ = included in model
pe = permanent environment   1 = 0 + linear slope fitted   - = not in model
bp = breeding paddock   2 = 1 + quadratic slope fitted
ss = service sire

Table 5.6   Random regression models with Log-likelihoods for mean chick weight production with the "best model" in bold

Model	Log-likelihood	-2 x LL Difference for models compared	Models compared	Residual	a	pe	bp	ss
1	-7316.71			6 422	-	-	-	-
2	-7 257.14	119.14	2 vs. 1	5 334	-	-	√	-
3	-7 025.98	581.46	3 vs. 1	2 813	-	-	-	√
4	-7 016.05	19.86	4 vs. 3	2 652	-	-	√	√
5	-6 824.80	382.5	5 vs. 4	1 775	√0	-	√	√
6	-6 842.78	346.54	6 vs. 4	1 784	-	√0	√	√
7	-6 824.42	0.76	7 vs. 5	1 779	√0	√0	√	√
8	-6 797.36	54.12	8 vs. 7	1 479	√0	√1	√	√
9	-6 806.84	35.16	9 vs. 7	1 445	√1	√0	√	√
10	singular				√1	√1	√	√
11	**-6 786.02**	**22.68**	**11 vs. 8**	**1 331**	**√0**	**√2**	**√**	**√**
12	-6 795.16	23.36	12 vs. 9	1 294	√2	√0	√	√

a = direct additive genetic effect   0 = intercept fitted   √ = included in model
pe = permanent environment   1 = 0 + linear slope fitted   - = not in model
bp = breeding paddock   2 = 1 + quadratic slope fitted
ss = service sire

Table 5.7   Random regression models with Log-likelihoods (LL) for percentage hatched with the "best model" in bold

Model	Log-likelihood	-2 x LL Difference for models compared	Models compared	Residual	a	pe	bp	ss
1	-6 152.59			583	-	-	-	-
2	-6 124.17	56.84	2 vs. 1	523	-	-	√	-
3	-6 049.28	206.62	3 vs. 1	392	-	-	-	√
4	-6 043.00	12.56	4 vs. 3	378	-	-	√	√
5	-6 022.14	41.72	5 vs. 4	343	√0	-	√	√
6	-6 012.23	61.54	6 vs. 4	340	-	√0	√	√
7	-6 012.20	19.88	7 vs. 5	340	√0	√0	√	√
8	-6 008.24	7.92	8 vs. 7	304	√0	√1	√	√
9	-6 001.79	20.82	9 vs. 7	305	√1	√0	√	√
10	singular				√1	√1	√	√
11	**-6 004.81**	**6.86**	**11 vs. 8**	**294**	**√0**	**√2**	**√**	**√**
12	-5 998.36	6.86	12 vs. 9	291	√2	√0	√	√

a = direct additive genetic effect   0 = intercept fitted   √ = included in model
pe = permanent environment   1 = 0 + linear slope fitted   - = not in model
bp = breeding paddock   2 = 1 + quadratic slope fitted
ss = service sire

Fitting the intercept and linear slope for a and pe effects (Model 10) resulted in all the analyses becoming singular (Tables 5.3 to 5.7). This finding suggests that a and pe were vying for the same information and were thus unable to resolve.
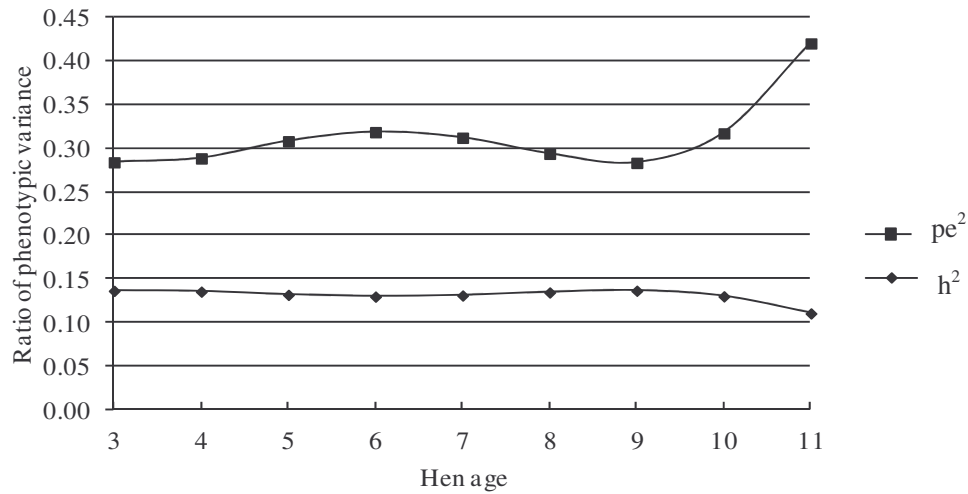
Figure 5.2 Direct heritability (h^2) and permanent environment (pe^2) as ratios of the phenotypic variance of total egg production for hen ages.

The direct genetic (h^2) and animal pe (pe^2) effects as ratios of the phenotypic variance (Figure 5.2) were calculated for EP from variance results from Model 11. The direct genetic effect was fitted as an intercept, and the animal pe effect was fitted as a quadratic polynomial with an intercept.

Estimates of h^2 were moderate and remained relatively constant, ranging from 0.13-0.14 for 3 to 10-year-old hens and decreasing to 0.11 for 11-year-old hens (Figure 5.2). The permanent environment variance ratio (pe^2) ranged from 0.28- 0.32 for 3 to 10-year-old hens, rising relatively steeply to 0.42 for 11-year-old hens.

In previous studies, estimates of h^2 and pe^2 as ratios of the phenotypic variance ranged from 0.12-0.29 and from 0.08-0.32 respectively when using repeatability models (i.e. fitting the intercept for both random effects; Table 5.8). The consistency between estimates was not unexpected, as some animals formed part of the previous analyses, summarized in Table 5.8. Mean variance ratios for service sire and bp both amounted to 0.05 as ratios of the phenotypic variance, and is consistent with previously published results.

Parameters for chick production are presented in Figure 5.3, with h^2 and pe^2 as ratios of the phenotypic variance ranging from 0.07-0.08 and from 0.29-0.41 respectively.

Trends for h^2 of EP and CP were similar in shape (Figures 5.2 and 5.3), and could be in part due to number of chicks to a large extent depending on the number of eggs produced.
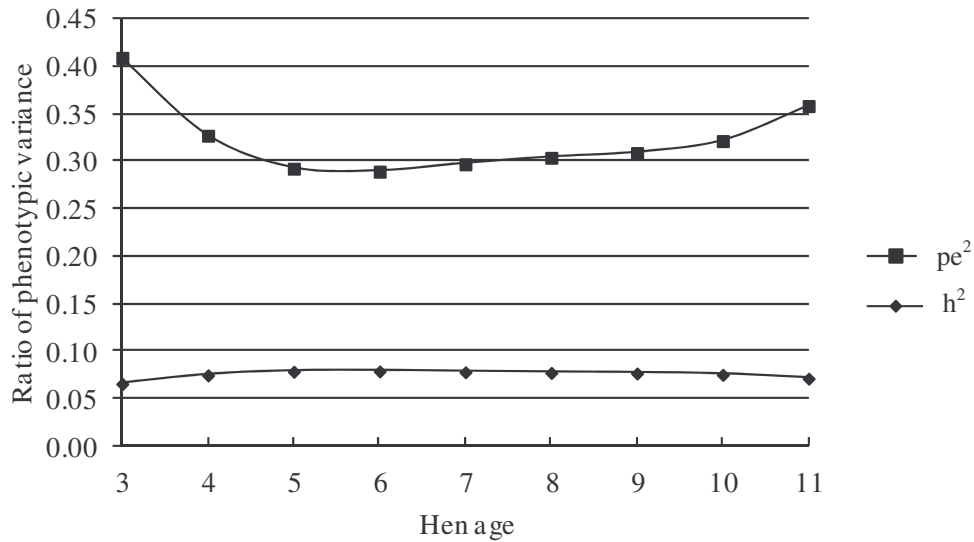
Figure 5.3 Direct heritability (h^2) and permanent environment (pe^2) as ratios of the phenotypic variance of total chick production for hen ages.

The lines depicted in Figures 5.4 and 5.5 largely mirrored one another in shape. Estimates for h^2 and pe^2 ranged from 0.49-0.61 and 0.17-0.33 for mean egg weight and from 0.37-0.45 and 0.21-0.35 for mean chick weight. MEW was highly heritable for all hen ages and MCW was moderately to highly heritable. Three- and four-year-old hens, as well as hens 10 years and older, had higher heritabilities than 6-, 7- and 8-year-old hens.
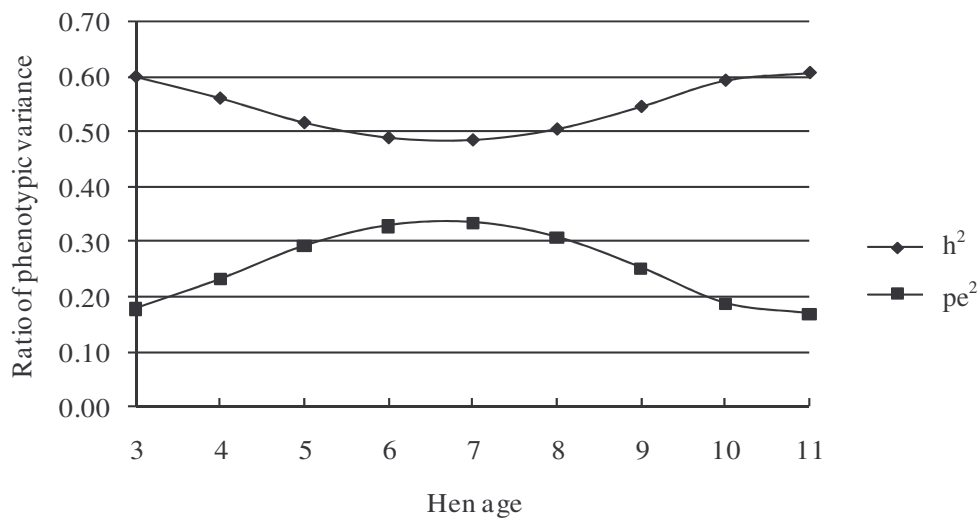

Figure 5.4 Direct heritability (h^2) and permanent environment (pe^2) as ratios of the phenotypic variance of mean egg weight for hen ages.
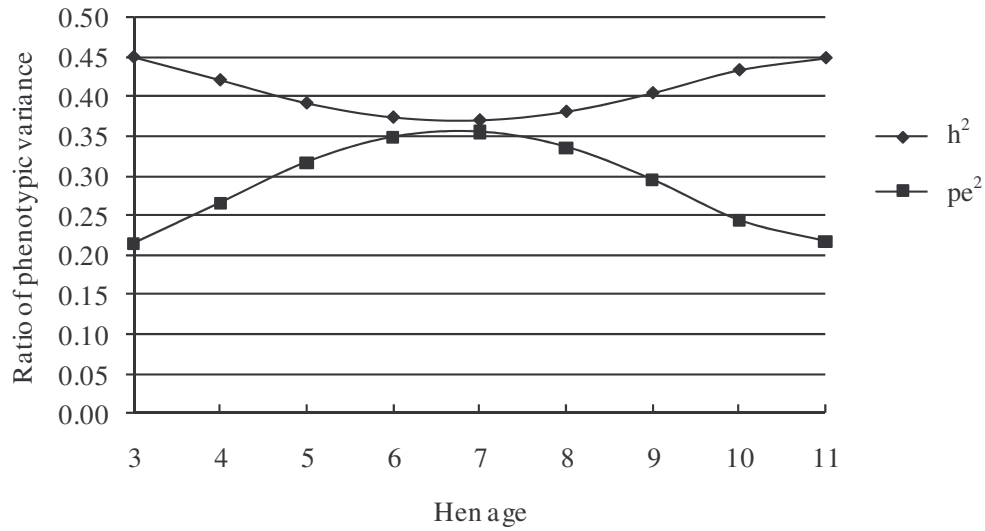
Figure 5.5 Direct heritability (h^2) and permanent environment (pe^2) as ratios of the phenotypic variance of mean chick weight for hen ages.
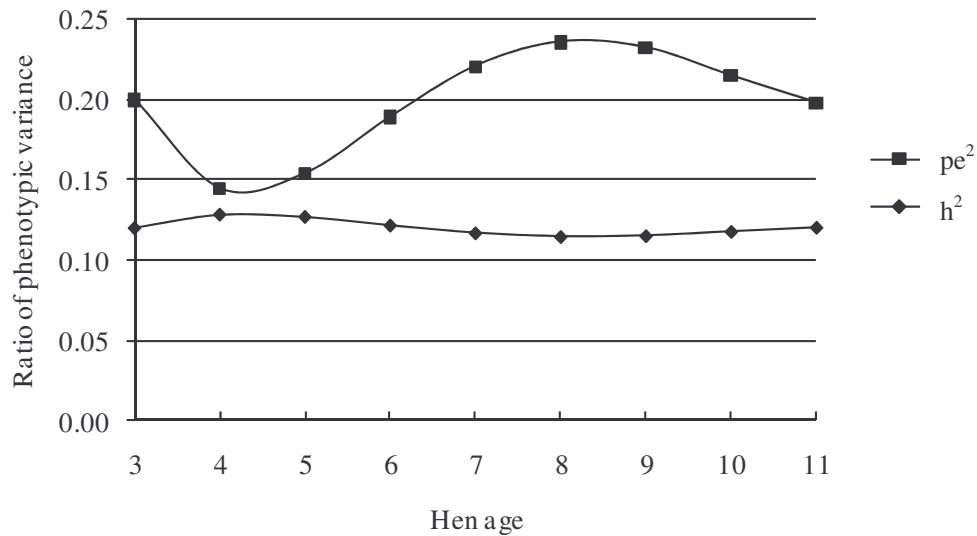

Figure 5.6 Direct heritability (h^2) and permanent environment (pe^2) as ratios of the phenotypic variance for hatchability for hen ages.

Estimates of h^2 and pe^2 ranged from 0.11-0.13 and 0.14-0.24 for H. Selection for hatchability is thus possible. All these parameter estimates are within the ranges of the literature values shown in Table 5.8.

Table 5.8 Summary of published heritability estimates and variance ratios (± s.e.) of egg, and chick production and quality traits of mean egg and chick weight and hatchability in ostriches

Trait and reference	n	σ^2_p	h^2	c^2_{pe}	c^2_{ss}
Egg production					
Bunter *et al*. (2001*a*)	708	580	0.12 ± 0.11	0.32 ± 0.10	n.a.
Cloete *et al*. (2004)	1177	-	0.26 ± 0.09	0.16 ± 0.08	n.a.
Cloete *et al*. (2005)	1487	477	0.29 ± 0.04	n.a.	0.07 ± 0.03
Fair *et al*. (2005)	7502	21	0.14 ± 0.03	n.a.	0.06 ± 0.02
Cloete *et al*. (2008b)[A]	1936	477	0.18 ± 0.06	0.17 ± 0.06	0.03 ± 0.01
Fair *et al*. (2011)[B]	13876	20	0.04 ± 0.02	0.08 ± 0.03	0.05 ± 0.01
Present study (2012)	1822	515-639	0.13-0.14	0.28-0.42	0.09 ± 0.01
Chick production					
Bunter *et al*. (2001*a*)	708	353	0.11 ± 0.11	0.33 ± 0.12	n.a.
Cloete *et al*. (2004)	1177	-	0.21 ± 0.08	0.18 ± 0.08	n.a.
Cloete *et al*. (2005)	1487	285	0.26 ± 0.11	n.a.	0.07 ± 0.03
Fair *et al*. (2005)	7502	11	0.14 ± 0.03	n.a.	0.09 ± 0.02
Cloete *et al*. (2008b)[A]	1936	285	0.17 ± 0.06	0.19 ± 0.05	0.05 ± 0.01
Fair *et al*. (2011)[B]	13876	10	0.05 ± 0.03	0.08 ± 0.03	0.06 ± 0.01
Present study (2012)	1822	269-323	0.07-0.08	0.29-0.41	0.10 ± 0.01
Mean egg weight					
Bunter *et al*. (2001*a*)	689	15273	0.43 ± 0.16	0.25 ± 0.12	n.a.
Cloete *et al*. (2004)	1062	-	0.72 ± 0.	n.a.	0.08 ± 0.03
Brand *et al*. (2008)	969	11327	0.44 ± 0.12	0.32 ± 0.11	n.a.
Fair *et al*. (2005)	5436	17110	0.59 ± 0.04	n.a.	0.08 ± 0.03
Fair *et al*. (2011)[B]	9446	20442	0.44 ± 0.04	0.09 ± 0.02	0.04 ± 0.01
Present study (2012)	1708	14806-18616	0.49-0.61	0.17-0.33	0.02 ± 0.01
Mean chick weight					
Bunter *et al*. (2001*a*)	624	7162	0.51 ± 0.17	0.25 ± 0.16	0.06 ± 0.04
Cloete *et al*. (2004)	957	-	0.74 ± 0.03	n.a.	0.07 ± 0.03
Cloete *et al*. (2005)	1212	6185-7883	0.71 ± 0.03	n.a.	0.08 ± 0.02
Fair *et al*. (2005)	4210	8372	0.56 ± 0.05	n.a.	0.11 ± 0.03
Brand *et al*. (2008)	963	6182	0.56 ± 0.11	0.21 ± 0.10	n.a.
Fair *et al*. (2011)[B]	7394	11321	0.67 ± 0.02	n.a.	0.04 ± 0.01
Present study (2012)	1548	7025-8567	0.37-0.45	0.21-0.35	0.10 ± 0.01
Hatchability %					
Cloete *et al*. (2005)	1365	599	0.05 ± 0.05	0.24 ± 0.06	0.19 ± 0.04
Fair *et al*. (2005)	7502	1110	0.20 ± 0.04	n.a.	0.12 ± 0.03
Cloete *et al*. (2006a)	1089	725	0.10 ± 0.07	0.21 ± 0.08	0.22 ± 0.05
Fair *et al*. (2011)[B]	9530	822	0.02 ± 0.02	0.11 ± 0.02	0.05 ± 0.01
Present study (2012)	1712	638-716	0.11-0.13	0.14-0.24	0.23 ± 0.01

The models fitted for Fair *et al.* (2005, 2011[B]) differed from those done previously, in that they were for monthly egg production data. h^2 = direct heritability, c^2_{pe} = permanent environmental variance as a proportion of phenotypic variance, c^2_{te} = temporary environmental variance as a proportion of phenotypic variance, c^2_{ss} = service sire variance as a proportion of phenotypic variance; σ^2_p = phenotypic variance. When a random effect was not part of the model used n.a. (not applicable) is indicated. [A]Derived from a three-trait repeatability model, involving mature female live weight, egg

production and chick production. [B]Derived from Mixed model for within breeding season. The present study used a mixed model random regression over years.

It is reasonable to assume that h² estimates derived from data accrued over an entire breeding season would exceed those derived from within season analyses, since the former data were found to be inherently more variable, this was also the case when comparing the present study with the results for H, as reported by Fair *et al.* (2011).

5.4   Conclusions

The main focus of this study was to determine if the h^2 of annual ostrich production differs for records obtained at different female ages, and whether final selection on own performance should be postponed until later ages. Under the model fitted, and with limited data heritability estimates for the quantitative production traits of EP and CP were largely independent of age. Selection on own performance could thus be conducted after 3-year-old records of females were recorded. Based on previous studies, such selection ought to lead to sustainable and additive genetic gains in egg and chick output.

Hens older than eleven years of age should be replaced with genetically superior younger (2- and 3-year-old) hens. Such a strategy would reduce the generation interval, giving more opportunities over time for selection of superior animals. Three-year-olds produced the highest mean number of chicks, suggesting that this trait is well-expressed at this stage. The quality traits, MEW and MCW had moderate to high h^2 estimates. These traits should thus respond to selection. However, optimum egg weights need to be determined with reference to incubator functioning and hatchability. Hatchability could be improved systematically by not allowing hen ages of >11 years, but would also respond to selection of superior hens ($h^2 = 0.11$-0.13).

6

GENERAL CONCLUSIONS

The objective of the study was to provide the South African ostrich industry with information on genetic and environmental parameters influencing production and reproduction of females within and across breeding seasons. This knowledge could then help in developing breeding programmes for the ostrich industry.

Pedigree structures of commercial ostrich flocks are unknown in South Africa, but it is believed that flocks are relatively old with few age groups. Analysis of the Oudtshoorn Research Farm ostrich resource flock revealed that the pedigree status of the ostrich flock were encouraging, as results indicated that there was a low rate of inbreeding and a relatively high effective population size. The current annual mean inbreeding was low at 0.51%. Obtained ΔF_i values are still subject to change due to shallowness of the analysed pedigree and thus require more generations of pedigree data for future monitoring of inbreeding. The flock had a relatively long mean generation interval of 7.7 years, which could be shortened to increase the rate of genetic improvement of economically important traits. It is concluded that the studied population had acceptable levels of genetic variability. Pedigree analysis of other ostrich flocks need to be done for comparative studies.

Variance and (co)variance components for genetic effects and non-genetic effects affecting performance traits EWT, CWT and H were estimated in this study. It was demonstrated that the fixed effects of year, month and their interaction year x month, dam age and, sequence the egg was laid in and contemporary group contribute significant to the traits measured and should thus be included in models to ensure accurate determination of genetic parameters. The random environmental effects of ce, pe and bp were also significant but low indicating that their inclusion in a model would be necessary when calculating genetic parameter of direct and maternal effects. The random genetic direct and maternal effects were also detectable and significant with moderate heritabilities indicating that genetic improvement in production traits in ostriches would be possible. The high positive correlation

between EWT, CWT and H shows that the industry can improve production unconstrained as yet by negative correlation as found in the poultry industry.

Age specific seasonal production patterns for ostrich females were shown to be significant indicating that seasonal production trends of 2-year-old females differed from those of older females. Potential candidates for selection can well be assessed for reproduction based on own performance and not only on maternal performance, as was the case thus far (Cloete *et al*., 2004). Hens in the age group categories of 3, 4, 5 and 6-7 years old outperformed 2 and 12+ year olds for the quantitative (CP and H) and qualitative (MEW and MCW) traits. Superior young hens should be identified and selected for replacement while hens older than 11-years old should be replaced. Three-year-old birds produced the highest mean number of chicks suggesting selection decisions on own performance could be taken at this stage. Heritabilities estimated indicate that reproduction traits analysed would respond favourably to selection pressure. High levels of hatching failure were observed, with only ~50% of eggs set eventually resulting in chicks. Further research regarding infertility and shell deaths is warranted. From this study it was clear that hatchability could be improved by genetic improvement due to selection of superior hens ($h^2 = 0.09$-0.13). From a systemic perspective care should be taken to reduce the average hen age while storage time before setting should be managed.

Random regression models were subsequently used to study the viability of early selection for increased EP and CP. The quality traits of MEW, MCW and H were also considered. Heritability estimates derived in this manner for egg and chick production were stable across hen ages and consistent with previous literature estimates using other methods. This method again indicated that selection of superior hens on own performance is feasible after three years. Older hens should be replaced with genetically superior younger (3-year-old) hens. This would reduce the generation interval and more replacement opportunities for the introduction of superior animals. The quality traits, MEW and MCW had moderate to high heritability estimates and should respond to selection. However, these traits may have to be selected for an intermediate optimum to ensure uniform incubator conditions for all eggs.

The recommendations from the current study are:

- Breeding programmes and structures to facilitate record keeping of performance and pedigree data need to be considered on a wider scale, as commercial production systems do not consider population structures at all. However this could change with advances such as AI and the usage of fewer males as parents. Experience in other livestock industries shows that AI leads to rapid genetic improvement but also in reduced population sizes and increased inbreeding levels. If the breeding structure changes to make more use of AI it should be a priority to continuously access level and rate of inbreeding. These records would then be available to monitor the pedigree status of the industry in terms of inbreeding, genetic diversity and generation interval nationally as well as the progress in production and reproduction traits.
- Seasonal mating of birds younger than 11-years of age should be encouraged to shorten the generation interval and to increase hatchability of the chicks.
- There was no evidence of serious unfavourable correlations between quantitative and qualitative traits. As all traits were heritable selection for improved production and reproduction is encouraged.
- Early identification and selection of superior birds should be used to shorten the generation interval resulting in increased and quicker response to selection.
- Increasing hatchability of eggs from the present low levels needs further research and improvements in this trait could impact on the overall profitability of ostrich farming. Increased number of chicks would also ensure a greater genetic pool from which breeding birds could be selected.

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