INTRODUCTION
The past few decades have been characterised by marked advancements in the genetic evaluation of livestock and sustained improvement of production traits, particularly in the more intensive industries (poultry, dairy cattle and pigs). The ostrich industry is a notable exception in this regard. A lack of knowledge both of genetic and environmental influences on production characterises the industry. Definite breeding objectives and industry breeding structures are absent. Further, characteristics typical of ostrich production systems present challenges for implementing genetic improvement programs (Cloete et al., 1998; Bunter and Graser, 2000) although these problems are not regarded as insurmountable. We present progress recently made on knowledge of the genetic basis of ostrich production traits in this review, hoping that it will stimulate further research. A number of issues that may hamper progress in the genetic evaluation of ostriches are also discussed. However, little or no information is provided with regard to history and background of the ostrich industry. Interested readers are referred to the literature (Cloete et al., 1998; Petitte and Davis, 1999; Bunter and Graser, 2001).

OSTRICH PRODUCTS
The commercial turnover of the ostrich industry is mostly based on leather, meat and feathers. Until recently, up to 70% of the income was derived from leather, with meat contributing 25% and feathers the remaining 5% (Cloete et al., 1998a). Due to an oversupply in the marketplace, leather prices are depressed at present and grading of very strict. Conversely, there is a good demand for ostrich meat owing to the BSE scare, shifting consumers towards alternative red meat sources. The contribution of the products to the income from ostriches has shifted accordingly. It is estimated that leather and meat contribute about equally (45% each) to the income of farmers, with feathers accounting for 10%. Progeny of the breeding flock largely accounts for the former two commodities. Breeding birds produce the best quality feathers.

PERFORMANCE LEVELS
Mean performance levels of traits generally recorded in ostriches are presented here. In view of constraints on space, only traits that may be used as part of a selection program, or that would be monitored to assess correlated responses, are considered. Readers requiring more information on other traits that have been evaluated are referred to the references provided.

Reproductive traits. Report measures of egg production, chick production and hatchability are extremely variable in the literature (Deeming, 1996; More, 1996b; van Schalkwyk et al., 1996; Bunter and Graser, 2000; Bunter et al., 2001a). Coefficients of variation exceeding
50% are frequently reported. More (1996b) reported a range of 0 to 90 eggs per female in Australian flocks. Survey results derived from approximately 90 international ostrich producers indicated a 0 to 118 eggs per hen (Bunter and Graser, 2000). Chicks hatched per hen range from 0 to 95. Bunter et al. (2001a) reported a production range of 0 to 121 eggs and 0 to 90 chicks for individual females over a eight month breeding period in South Africa. Incubation results for commercial ostrich hatcheries were recently summarised by Deeming and Ar (1999). From the sources cited in their review, fertility of ostrich eggs ranged from 30 to 87 % while hatchability of fertile eggs ranged from 11 and 80 %. More recently, Bunter and Graser (2000) reported a mean figure of 20 % for infertility (range : 0 to 75 %). The average hatching percentage of all eggs set was 64 % in this survey (range : 17.5 and 99 %).

Egg and chick traits. The average weights of ostrich eggs are around 1.4 kg (Deeming, 1996; Cloete et al., 1998a; 2001; Bunter et al., 1999; Bunter and Graser, 2000) with coefficients of variation slightly above 10 %. Evaporative water loss to 35 days of incubation was roughly 15%, with a coefficient of variation of slightly above 20 % (Blood et al., 1998; Cloete et al., 2001). Average values for day-old chick weight approximated 0.85 kg, with coefficients of variation around 12 to 15 % (Cloete et al., 1998a; 2001; Bunter et al., 1999; Bunter and Graser, 2000). Verwoerd et al. (1999) suggested that day-old chick weights of 0.78 to 0.96 kg could be regarded as good quality ostrich chicks, providing factors known to have detrimental effects on chick survival and performance (e.g. oedema, dehydration, egg transmitted diseases) are absent.

Overall levels of chick mortality in the literature were found to be high and variable (More, 1996a; Cloete et al., 2001; 2002). Values cited from the literature ranged from close to 0 % mortality to cases where all chicks have died. Survey results derived from 103 producers participating in the study reported by Bunter and Graser (2000) suggested that ostrich chick mortality to one month averaged 16.9 % (range : 0 to 90 % across flocks). Corresponding values at three months of age were 26.2 % (range : 1 to 100 %).

Later live weights and slaughter traits. In South Africa, birds have historically been slaughtered at approximately 14 months of age. The average weight of ostriches at this age was approximately 110 kg, with a coefficient of variation of approximately 12 % (Cloete et al., 1998a; 2001; Bunter et al., 1999; Bunter and Graser, 2000). However, it is possible to obtain similar weights in younger birds with diets aimed at maximising growth rates (Cilliers, 1995). Skin area was 113 and 126 dm² in studies where it was considered (Cloete et al., 1998a; 1998b). The mean live weight and standard deviations of mature breeding male and female birds are consistent with means presented for slaughter weight (van Schalkwyk et al., 1996).

ENVIRONMENTAL FACTORS AFFECTING PERFORMANCE

Several authors have reported significant season or production year effects on the reproductive performance of ostriches (van Schalkwyk et al., 1996; Bunter and Graser, 2000; Bunter et al., 2001a) and subsequent chick mortality (Cloete et al., 2002). Such effects are expected generally, but are largely of academic interest in the absence of identifying specific factors that affect performance, and are not discussed further.
Reproductive traits. Egg and subsequently chick production increases with hen age to peak at 7 to 10 years (Cloete et al., 1998; Bunter et al., 2001a), and subsequently declines in later years. The reduced performance of older hens was more pronounced for chick production. Hens older than 10 years did not produce more chicks than 2-year old hens (Bunter et al., 2001a). Compared to two-year old hens, mature hens at peak performance produce an additional 20-25 eggs (or 10-15 chicks) per season. Chick production is also influenced by male performance. Infertility of eggs was associated with the age of the service sire (Bunter et al., 2001). Very young males (2 year olds) produce a higher percentage of infertile eggs than older males, with 3 to 9 year old males demonstrating good fertility. Conversely, the mates of service sires older than 8-9 years produced as many infertile eggs as mates of 2-year old sires. Differences in individual ages of hens and their mates, and flock age structure, almost certainly contributed to some of the variation that is observed in the mean levels of reproductive performance.

Egg and chick traits. Egg and chick weights change with hen age in a curvilinear fashion, peaking in 4 - 5 year old hens, and followed by a steady decline at later ages (Bunter et al., 2001a). Hens older than 11 years generally produced lighter chicks than two-year old hens. The position of the egg in the laying sequence also affected egg and chick weights (Bunter and Graser, 2000). Egg weight increases rapidly for the first five eggs produced in the laying sequence, followed by a more gradual increase. This trend was less evident for chick weights, which tended to stabilize at approximately 90 - 100 g heavier than chick weights recorded for chicks produced from eggs laid earlier in the laying sequence.

Chick mortality to 28 days of age was affected by egg weight, day-old chick weight and evaporative water loss (Cloete et al., 2001 ; More, 1996). Low live weight chicks hatching from small eggs were particularly at risk of dying prior to 28 days of age. Chicks that hatched from eggs showing excessive evaporative water loss were also more likely to succumb. Low live weight chicks at 28 days were also at risk of dying before reaching an age of three months.

Later live weights and slaughter traits. Sex effects were rarely found to be significant (Cloete et al., 1998a ; 1998b ; Bunter et al., 1999 ; Bunter and Graser, 2000). Female slaughter animals produce the same drumstick weight and skin area as males when slaughtered commercially (Cloete et al., 1998b).

PARAMETER ESTIMATES
Parameter estimates production in farmed ostriches have only recently become available. Most estimates have been obtained from the same source population at different times, resulting in fairly consistent values. There is a need for similar analyses on other populations.

Reproductive traits. The pair-breeding mating structure of the ostrich flock considered complicates the partitioning of variances attributable to hen genetic effects, hen permanent environmental effects and service sire effects. In the first analyses, these effects were fully confounded with mating paddock (van Schalkwyk et al., 1996 ; Cloete et al., 1998). Initial reports featured between hen variance ratios (repeatability), encompassing genetic and non-genetic effects mentioned above. Estimates ranged from 0.38 to 0.56 for reproductive traits.
included in these analyses (van Schalkwyk et al., 1996; Cloete et al., 1998a). As established breeding pairs were introduced to different breeding paddocks, and females and males with more than one mate increased, it became feasible to separate variance components. Sampling correlations between these effects still reduce the ability to partition effects accurately. Reproductive traits were estimated to be lowly heritable, $h^2$ estimates being slightly higher than 0.10 in most cases (Bunter and Graser, 2000; Bunter et al., 2001a). The exceptions are estimates of $h^2$ for average egg and chick weights, which tend to be much higher than those for the other reproductive traits (Bunter and Graser, 2000; Bunter et al., 2001a). After accounting for effects such as hen age, permanent environment effects due to the hen ($c^2$) accounted for over 30% of the overall phenotypic variation in reproductive performance. Individual service sires also contributed to variation in overall reproductive performance, mainly through their effect on the number or percentage of infertile eggs produced.

Egg and chick production traits are highly correlated as expected, but correlations between random effects are not unity (Bunter and Graser, 2000; Bunter et al., 2001b). The number of eggs produced that were infertile exerted a negative influence on chick production, mainly through a strong negative correlation between these traits for service sires. Correlations between egg or chick production and average egg or chick weights were low to moderate and positive in sign, indicating no unfavourable associations currently between these traits. Correlations of average egg weight with average chick weight were high throughout.

Little information is available on specific underlying traits that contribute to reproductive success of hens. However, shell deaths (a measure of reproductive failure) was related to differences in evaporative water loss of eggs during incubation (Blood et al., 1998). Higher shell death rates were found in eggs showing very little or excessive water loss to 35 days of hatching. Evaporative water loss is repeatable for hens (Blood et al., 1998), providing evidence for the importance of shell quality traits in determining reproductive outcomes.

Parameter estimates obtained for ostriches are in general agreement with results summarised for similar traits in poultry (Kinney, 1969; Crawford, 1990; Koerhuis and McKay, 1996). These estimates suggest that culling of individual females with poor reproductive performance will improve reproduction in the current flock. Solutions for service sire could be used to cull infertile service sires. It also seems probable that future genetic improvement through selection will be achieved in ostriches. The profitability of ostrich farming could be markedly enhanced through the improvement of reproduction, by taking these factors into account.

**Individual egg weight, day-old chick weight and chick survival.** Estimates of $h^2$ were ≤0.20 for egg and day-old chick weight (Bunter et al., 1999; Bunter and Graser, 2000). Sizeable $m^2$ and $c^2$ variance ratios (0.24 to 0.31) were also evident in the study of Bunter and Graser (2000). Large overall effects due to the hen were observed, contributing to more than 50% of the total phenotypic variation. The repartitioning of variation from breeding paddock in the study of Bunter et al. (1999) to maternal variation in the study of Bunter and Graser (2000) can be attributed to the relocation of females to other breeding paddocks, facilitating the repartitioning of variances. Added pedigree depth in the larger data set could also have contributed. Adequate genetic variation for progress by parental selection thus exists in the case of ostrich egg and
day-old chick weights. However, the conflict between optimising egg weights for artificial incubation, and increasing chick weight to improve survival, make it unclear what improved performance for these traits would constitute. Preliminary parameter estimates on chick survival suggest that there is limited genetic variation for this trait (Cloete et al., 2002). Estimates of $h^2$ were generally not different from zero. Significant $m^2$ estimates ranged from 0.03 to 0.05, depending on the type of analysis and modelling for the effects of chick weight.

**Later live weights and slaughter traits.** Estimates of heritability for weight are moderate in magnitude. The exception is live weight at three months, for which no significant additive variation was apparent (Bunter et al., 1999; Bunter and Graser, 2000). These studies provided evidence for a significant common environmental ($c^2$) effect of the hen on the performance of her full-sib offspring. In multi-trait analyses containing records for egg, chick and later weights (Bunter, 2002) this effect was reduced to less than 10% of the observed phenotypic variance, and would appear to at least partially result from differences in chick weight at hatching (largely induced by between hen variation in egg weight). Selection for juvenile live weights will thus be less effective if the effects due to the hen on live weight are not accounted for.

Genetic correlations between egg or chick weight and later weights were generally low and not different from zero, while environmental and phenotypic correlations were low and positive (0.10 to 0.17; Bunter and Graser, 2000). Conversely, live weight at 6 months, 10 months and slaughter were highly correlated. Genetic correlations between these weights were not different from unity. Phenotypic correlations were also high (0.57 to 0.78), becoming smaller with an increase in the interval between measurements. Selection decisions for the improvement of live weight can be taken at fairly early ages (≥6 months). Estimates of $h^2$ from multi-trait analyses (Bunter, 2002) were generally higher than those obtained from single trait analyses (Bunter and Graser, 2000). This outcome suggests that birds carried through to later weights were selected. However, no specific culling program was in place. Consequently, parameters are likely influenced by natural selection as mediated by the high early chick mortality.

One important omission in the knowledge of genetic parameters for economically important traits are estimates for skin traits. Phenotypically, skin area is closely related to slaughter weight (Cloete et al., 1998b). It is reasonable to assume that genetic parameters for the two traits would be associated. However, genetic parameters for skin quality traits have not been estimated so far due to a lack of suitable data. Results on feather traits are generally not found in the literature, although Louw and Swart (1982) reported that the number of quills on the wings of ostriches is moderately heritable.

**OTHER CONSIDERATIONS**

This review has, so far, dealt with performance levels for production traits, environmental factors of significance, and summarised parameters. It would, however, be incomplete without reference to some of the issues facing the ostrich industry. We briefly touch on some of these.

**Industry Breeding Structures.** The relatively poorer reproductive performance of young hens and cocks, a low female : male ratio, the capital required for constructing small mating paddocks or implementing parental identification systems, and the costs of performance...
recording impose a significant financial burden on ostrich breeders. If a clue could be taken from the poultry industry, the provision of genetic improvement in ostriches should probably be centered around relatively few breeding flocks which provide stock for commercial producers.

Assuming no conclusive genetic antagonism between reproduction and growth – van Schalkwyk et al. (1996) found a phenotypic correlation of -0.07 between hen live weight and chick production – selection for growth and reproduction may be achieved in a single dual-purpose line. Breeding could also be structured in specialist lines selected for reproduction or slaughter traits. This concept has previously been contemplated (Cloete et al., 1998a; Petitte and Davis, 1999). Commercial production could be based on the crossing of lines in a terminal crossbreeding system. Research into the crossbreeding of various lines constituting the current commercial ostrich population should be conducted. At present, there is a tendency to crossbreed Kenyan Rednecks, Zimbabwean Blues and South African Blacks in a random fashion (Petitte and Davis, 1999), without any evidence of ‘breed’ effects or levels of heterosis to guide crossbreeding decisions.

Performance recording. Bunter and Graser (2000) highlighted the lack of basic pedigree and performance data for this species. To our knowledge, no formal ostrich recording scheme is presently in operation. Reasons for this include industry novelty and youth in most parts of the world combined with production systems (e.g. colony breeding) that complicate recording.

Recording of pedigree details or reproductive performance of individual hens is hard to achieve when many producers use colony breeding systems, whereby a number of females lay eggs in the same nest (Cloete et al., 1998a). Visits of individual females to the nest could be monitored electronically, and this would enable egg production to be recorded on an individual basis (for selection and culling purposes) as well as providing maternal pedigree. More sophisticated alternatives include DNA parentage determination. However, no commercial DNA pedigreering service for ostriches is in operation at present, and a lack of long-term stability in the industry probably constrains developments in this regard.

The recording of pedigree information from pair breeding flocks is an alternative to colony breeding. This system has been shown to facilitate the recording of data useful for genetic evaluation (Bunter and Graser, 2000). However, to fully exploit this potential traditional beliefs held by producers need to be sacrificed and some consideration to options for increasing selection intensities are required. Producers believe that maximum productivity is obtained if established pairs are mated from year to year in the same breeding paddock. This practice compromises the ability to separate male, female and potential breeding paddock effects, as was noted previously. Bunter et al. (1999) showed that a new mate in different seasons did not significantly reduce reproduction of mature hens, although this may not be the case for younger hens or if changes to mates occurred within the breeding season. Nevertheless, opportunities do exist to improve data quality through reallocating mates to different pairs, and paddocks, from year to year. Relative to small poultry species and other large livestock, selection intensities within this species are also substantially reduced on the male side. The introduction of a
workable system for artificial insemination is being investigated by several researchers (Malecki et al., 1997). This development could simplify ostrich breeding (Cloete et al., 1998a).

From our experience, eggs laid in a breeding operation should form the basis of recording reproductive data. The fate of each egg entering the system needs to be known (Bunter and Graser, 2000) to distinguish egg from chick production. Chick survival and growth (weight) to slaughter age are other important traits. The recording of at least one live weight between day-old and slaughter weights is proposed initially (Bunter and Graser, 2000). Once commodity markets and the industry have stabilised, it will be possible to determine more accurately the relative importance of performance recording additional weight, skin and meat quality traits.

Breeding objectives. There is no formal breeding strategy with well-established breeding objectives (Petitte and Davis, 1999; Bunter and Graser, 2000). With meat and skins the major sources of income, the production of a significant number of good quality chicks surviving to slaughter has to be considered the prime selection objective. Growth and feed efficiency are also important for efficient meat production, and for producing skins with an acceptable size. The combination of number of chicks (quantity) and day-old chick weight (quality) as weight of day-old chicks produced is a simple trait that could be considered, providing performance recording is adequate to distinguish between healthy versus diseased (e.g. oedema) chicks. The South African sheep industry has introduced this concept to good effect (Olivier, 1999), and the heritability of this trait was similar to that of other reproduction traits (~0.1: Bunter and Graser, 2000). Better stability and information on costs and returns would enable the development of more effective breeding objectives and their accompanying selection indices.

CONCLUSIONS
This review provides information on the genetic basis for most traits of economic importance in ostriches. Parameters are generally consistent with those derived for similar traits in poultry (Kinney, 1969; Crawford, 1990; Koerhuis and McKay, 1996) Genetic progress can generally be expected from implementing selection strategies. There are a number of notable omissions regarding genetic parameters for ostriches, including incubation parameters, skin traits and feather production. This information will be accumulated with time, enabling the development of a structured breeding plan which will maximise economic returns to the industry through breeding. Future structures of the breeding industry and the identification of all traits to be recorded are aspects that require further attention. Furthermore, it is clear that production difficulties constrain progress. A prime example is the poor chick survival often observed in the intensive, commercial production system (Cloete et al., 2001; 2002). Such issues need to be resolved for the industry to realise its full potential regarding to genetic improvement.

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