RELATIONSHIPS BETWEEN MEASURES OF REPRODUCTIVE PERFORMANCE IN FARmed OSTRICH HENS

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SUMMARY
Complete egg production data from a pair breeding flock located in South Africa were used to generate annual reproductive records for all hens exposed to breeding. Correlations between each pair of traits for individual animal (hen or mate) and environmental effects were estimated from bivariate analyses. Correlations between hen effects contained both genetic and permanent environmental effects, which were impossible to separate accurately for most traits. Random effect models differed between traits, but generally correlations between traits for the relevant random effects (hen, mate or environment) were similar in magnitude and direction. Exceptions were those between the number of clutches laid and other traits, where correlations between hen and environmental effects contrasted. Delayed commencement of lay at the start of the breeding season, short duration of lay, and increased clutching by hens were unfavourably correlated with annual egg and chick production. No antagonistic correlations were evident between egg production traits and average egg or chick weights in these data, although such relationships are commonly reported in other domestic poultry species. Increased data quantities, and improved data structure, are required to estimate genetic correlations between traits in this species.

Keywords: correlation, clutch, laying pattern, egg production, egg weight.

INTRODUCTION
In most farmed species, overall profitability is determined by performance in more than one economically important trait. As a consequence, breeding programs rarely focus on improvement in a single trait only, and knowledge of the associations between traits becomes important. Non-zero correlations between traits imply that selection or culling for one trait will affect performance levels in other traits. Antagonistic genetic correlations between traits are the most problematical from a breeding perspective, through potentially limiting response in the aggregate genotype and requiring action to avoid undesirable correlated responses under the selection process. The objective of this study was to investigate general relationships between measures of reproductive performance in farmed ostrich hens, as it was known in advance that the data did not support accurate estimation of genetic correlations between most traits.

MATERIALS AND METHODS
Information on the data used, trait definitions, characteristics of the traits, and models for analyses were presented in a companion paper (Bunter et al., 2001), and are not repeated here. Traits analysed in this study included annual records for: time (days) taken to commence laying (TTL) and duration...
of lay (DUL); number of clutches laid (NCL); number of eggs laid (NLAID), incubated (NINC), infertile (NINF) or hatched (NHAT); and average egg (EWT) and chick (CHWT) weights.

**Analyses.** Fixed effects models for each trait were as described in Bunter et al. (2001). Correlations between random effects for each pair of traits were estimated from a series of bivariate analyses performed using ASREML (Gilmour et al. 1998). This software was used to estimate variance components under mixed models by restricted maximum likelihood and to approximate standard errors for parameter estimates (Gilmour et al. 1995).

In previous studies a Likelihood Ratio Test (LRT) was used to assess the suitability of alternative random effect models for each trait. Results from each LRT (not presented) indicated that accurate separation of additive genetic from permanent environmental effects of the hen was not possible for most of the traits examined in this study. Consequently, a single random effect pertaining to each hen and trait were used in bivariate analyses. Additive relationships between hens were not explicitly modelled in order to allow for repeated records of each hen, which was the dominant structure in this data. Within animal correlations (which contain both additive genetic and permanent environmental effects) are subsequently presented from these analyses.

**RESULTS AND DISCUSSION**

Generally, estimates of correlations between random effects for each pair of traits were similar in magnitude and direction for both animal (hen or mate) and environmental effects (Table 1). The exceptions were correlations between NCL and the other traits for hen versus environmental effects, which are discussed further below.

Delayed commencement of lay at the start of the season (high TTL) was adversely related to total duration of lay, along with measures of egg and subsequently chick production. Correlations with average egg or chick weights were also negative. Conversely, increased duration of lay had the opposite effects and, given the greater magnitude of correlations between DUL and the other traits, was more important for predicting reproductive output than TTL alone. At the environmental level an increase in NCL was positively associated with the duration of lay and egg production. However, at the level of the individual hen, increased NCL (increasing pauses between eggs) adversely affected both egg and chick production. Thus, the pattern of lay had significant outcomes for reproductive success in individual ostrich hens. This was less evident when observed at the phenotypic level where only the negative correlation between NCL and NHAT was significant.

Correlations between NLAID and NINC did not differ from unity according to a LRT, indicating that these effectively were the same trait. Egg production was highly correlated with chick production through setting an upper limit for the latter, particularly at the level of the individual hen. Nevertheless, negative correlations between the number of infertile and hatched eggs illustrate the importance of egg fertility on final chick production. The negative correlation between egg infertility and the number of chicks that hatched was of greater magnitude for males than females, supporting egg fertility as a predominantly male mediated effect. The temporal distance between measures of egg and chick production are also associated with the intervening processes of egg collection, storage and incubation. Unrecorded differences in the management of individual eggs may have influenced
results for these data. Further, variation in characteristics inherent to eggs from individual hens (eg. egg and shell quality traits), and the subsequent suitability of incubation management for different eggs on hatchability, probably accounted for the less than unity correlations between either egg production or fertility and the number of chicks produced.

Correlations between egg or chick production with egg or chick weight were generally positive. In contrast, negative correlations between measures of egg production and egg weight are commonly reported for domestic poultry species (Kinney 1969). This difference may be related to differences between ostriches and small poultry in aspects of their reproductive biology. For example, the annual egg mass produced by the modern hen is considerably higher per unit body weight than that of ostrich hens, suggesting that resources and energy expenditure are more limiting for the high producing hens, thereby inducing reduced egg weight with increasing output. Further, correlations between reproductive traits in poultry are usually estimated from the first production cycle only. Our study contained repeated records from hens recorded over years, diluting the influence of variation in the achievement of sexual maturity during the first cycle of lay on both egg production and weight recorded. This effect may also partially account for the negative correlations between egg production and weight in domestic poultry. Chick weight at hatch is closely related to egg weight in ostriches, as is the case in other avian species (Kinney 1969).

CONCLUSIONS
At the level of the individual hen, chick production recorded at hatch is highly correlated with egg production and adversely influenced by delayed commencement of laying, short duration of lay, and increased clutching behaviour. Correlations between measures of egg production and average egg or chick weights were generally positive, but not always different from zero. These results provide preliminary evidence for a lack of antagonistic associations between reproductive traits of farmed ostrich hens, although genetic correlations remain unknown. Further, other potentially important reproductive traits, such as aspects of egg quality and chick survival, were not examined. An increased quantity of data, with improved structural characteristics, is required to accurately estimate genetic correlations between economically important reproductive traits for this species.

ACKNOWLEDGEMENTS
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REFERENCES
Table 1. Estimates of correlations between reproductive traits are presented above the diagonal for hen (bold font), mate or service sire (italics) and environmental effects (normal font), with phenotypic correlations below the diagonal (na: parameter not applicable, standard errors in parenthesis)

<table>
<thead>
<tr>
<th></th>
<th>TTL</th>
<th>DUL</th>
<th>NCL</th>
<th>NLAID</th>
<th>NINC</th>
<th>NINF</th>
<th>NHAT</th>
<th>EWT</th>
<th>CHWT</th>
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<tbody>
<tr>
<td>TTL</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DUL</td>
<td>-.67 (.02)</td>
<td>.27 (.23)</td>
<td>.79 (.06)</td>
<td>.69 (.02)</td>
<td>.16 (.18)</td>
<td>.48 (.04)</td>
<td>.21 (.12)</td>
<td>.08 (.12)</td>
<td></td>
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<tr>
<td>NCL</td>
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<td>.40 (.04)</td>
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<tr>
<td>NLAID</td>
<td>-.48 (.03)</td>
<td>.72 (.02)</td>
<td>-.03 (.05)</td>
<td></td>
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<tr>
<td>NINC</td>
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<td>.69 (.02)</td>
<td>-.06 (.05)</td>
<td>.99 (.001)</td>
<td>.04 (.19)</td>
<td>.87 (.04)</td>
<td>.25 (.10)</td>
<td>.05 (.10)</td>
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<td>NINF</td>
<td>-.13 (.04)</td>
<td>.17 (.04)</td>
<td>.03 (.04)</td>
<td>.22 (.05)</td>
<td>.23 (.05)</td>
<td></td>
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<tr>
<td>NHAT</td>
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<td>-.12 (.04)</td>
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<td>-.37 (.04)</td>
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<tr>
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<td>.24 (.04)</td>
<td>-.02 (.05)</td>
<td>.29 (.05)</td>
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<td>-.02 (.05)</td>
<td>.26 (.05)</td>
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<tr>
<td>CHWT</td>
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<td>.10 (.05)</td>
<td>-.02 (.05)</td>
<td>.11 (.06)</td>
<td>.12 (.06)</td>
<td>-.09 (.06)</td>
<td>.19 (.06)</td>
<td>.87 (.02)</td>
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</table>

TTL: time to lay (days); DUL: duration of lay (days); NCL: number of clutches laid; NLAID: number of eggs laid; NINC: number of eggs incubated; NINF: number of infertile eggs; NHAT: number of eggs which hatched; EWT: average egg weight; CHWT: average chick weight.