

## ORIGINAL ARTICLE

# Quantitative analysis of production traits in saltwater crocodiles (*Crocodylus porosus*): I. reproduction traits

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## Summary

Repeatability and phenotypic correlations were estimated for saltwater crocodile reproductive traits. No pedigree information was available to estimate heritability or genetic correlations, because the majority of breeder animals on farms were wild-caught. Moreover, as the age of the female breeders could not be accounted for, egg-size measurements were used as proxies. The reproductive traits investigated were clutch size (total number of eggs laid), number of viable eggs, number of eggs that produced a live, healthy hatchling, hatchability, average snout-vent length of the hatchlings and time of nesting. A second data set was also created comprising binary data of whether or not the female nested. Repeatability estimates ranged from 0.24 to 0.68 for the measurable traits, with phenotypic correlations ranging from -0.15 to 0.86. Repeatability for whether a female nested or not was 0.58 on the underlying scale. Correlations could not be estimated between the measurement and binary traits because of confounding. These estimates are the first published for crocodilian reproduction traits.

## Introduction

Isberg *et al.* (2004) and MacNamara *et al.* (2003) presented a detailed overview of the Australian crocodile industry. Briefly, it is based on the production of saltwater crocodiles (*Crocodylus porosus*) for the international skin trade. For those animals, the skins of which meet the requirements of an export-quality, first-grade skin, 80% of the total product value is derived from the sale of the skin, with the remaining 20% derived from the sale of meat (15%) and by-products (5%; backstrap, head/skull, feet). The major export destinations for Australian skins are France, Italy, Japan and Singapore to be manufactured into luxury fashion items such as handbags and shoes (MacNamara *et al.* 2003). Currently, the Australian industry is small, supplying only 1% of

the global market of crocodilian skins [Department of Transport and Regional Services (DOTRS) 2001]. Despite this, saltwater crocodile skins, with their relatively small scales, evenly distributed belly-scale pattern, and lack of bone deposits (osteoderms) in the belly scales, attract a premium price in comparison with the skins of other crocodilian species.

The Australian crocodile industry relies heavily on the harvesting of wild-collected eggs for the rearing of juveniles for the skin market. However, some farms also maintain a population of captive breeding animals with resultant offspring also being placed into the production system. Whilst there have been numerous biological studies to investigate the environmental effects on the reproductive characteristics of saltwater crocodiles, this study aims to obtain phenotypic parameter estimates for

various reproductive traits for inclusion in a multi-trait genetic improvement programme. The pedigree structure precludes estimation of heritability, so repeatabilities are estimated instead to set an upper bound. Genetic correlations cannot be evaluated with the available data set.

Isberg *et al.* (2003) defined four main selection objectives for crocodile reproductive efficiency, namely breeder output (number of live, healthy hatchlings per female per year), annual nesting of females, earlier nesting within a breeding season, and age of sexual maturity. Selecting for breeding animals that produce more hatchlings per year is an obvious way of increasing efficiency on a 'per breeder' basis because the overhead costs of breeder maintenance is reduced proportionally. There is anecdotal evidence that some females miss nesting every third or fourth year. Time of nesting within a year is important because the time when the offspring hatch is important in relation to seasonal effects on subsequent juvenile growth. Age of sexual maturity is currently seen as a low priority because only a few crocodiles have been raised in captivity for this purpose.

Under natural and farmed conditions, saltwater crocodiles in northern Australia nest primarily during the wet season between late October and April (Richardson *et al.* 2002). A female lays only one clutch of eggs in a nesting season. The eggs are laid during a single laying event, normally at night or early in the morning, into a previously constructed mound nest.

Not all eggs laid in a clutch produce a viable hatchling. Some eggs will be infertile, whilst others will die during incubation. Whilst high embryo mortality caused by flooding, predation or overheating are reported in the wild (Richardson *et al.* 2002), the chances of these adverse events are greatly reduced in captivity although not negligible. Using artificial incubation techniques (32°C; 90–100% relative humidity), time to hatch is approximately 80 days, which corresponds to a hatching period between February and June (Richardson *et al.* 2002).

## Material and methods

### Animals and data collection

Nesting records were collected from Janamba Croc Farm (Northern Territory, Australia) for the consecutive breeding seasons between 1994 and 2002. Data were collected from 30 pairs kept mostly in unitized (one male, one female) breeding pens, although some pens consisted of one male and two females.

With the exception of one pair, all breeding animals were wild-harvested. This had two implications. First, the age structure of the breeding population could not be ascertained and therefore, statistical adjustments for age could not be made. Secondly, only a few captive-born juveniles have been raised to become replacement breeders and as such, no familial data were available for the traits between generations. Therefore, this data set contains only repeated measures on individuals for the reproductive traits of interest. All adults were assumed to be unrelated and were kept as permanent breeding pairs for the data collection period.

The breeding animals were maintained in two types of pens: the B- and UB-pens. The B-pens contain a single male and single female, whilst the UB-pens usually have a single male and one to two females. The B-pens are much smaller (144 m<sup>2</sup>) in comparison with the UB-pens (600–800 m<sup>2</sup>). The UB-pens are considered to better mimic the natural environment with deeper water (up to 5 m) and adequate basking banks allowing the animals to regulate their own body temperature. In contrast, the B-pens have two small water ponds with one being slightly larger than the other and no more than 1 m deep. Under tropical conditions, the animals in the B-pens do not have the same thermoregulatory behaviour patterns available as the UB-pen animals. The possible inability to thermoregulate as effectively could affect the developing embryos during the period of 4–8 weeks between mating and oviposition (Lang 1980). The second water pond in the B-pens provides a refuge for the females, which are sometimes subject to lethal or damaging male aggression. Two of the females included in this study were seriously injured by their male partners. Breeding crocodiles are fed once a week, generally receiving either one chicken each or equivalent in red meat.

The standard practice on the farm is to collect the eggs within 24 h of oviposition to minimize embryo mortality. Daily monitoring is undertaken to observe any nests being constructed. Nests are carefully opened until the nest cavity (where all the eggs are laid) is exposed. Each egg is marked along the dorsal midline to indicate its 'upright' position within the nest so that it can be incubated in the same orientation as rotating the egg causes the embryo to 'suffocate' from the egg contents (Ferguson 1985). Infertile eggs are detected by 'candling' with a small torch. Eggs that have been collected within the first 24 h after laying are still translucent and infertile members of the clutch are recognized by the absence

**Table 1** Crocodilian reproductive traits of economic importance

	Abbreviation	Description
Clutch size (eggs)	ClSize	Total number of eggs collected in a clutch
Number viable (eggs)	NoViable	ClSize minus the infertile eggs and those that died before collection
Number hatch (hatchlings)	NoHatch	NoViable minus the those that died during incubation or were euthanased due to abnormalities (lethargy, kinked spine, external yolk sac, external organs, etc.)
Hatchability	HatchR	NoHatch as a proportion of ClSize
Average snout–vent length (mm)	AvSVL	Average of a random sampling of 10 hatchling SVL (approximately 30%) from each clutch. The animals were inverted and the tip of the snout placed at the beginning of a clear, plastic ruler and the measurement was taken to the nearest 1 mm
Hatch days (days)	HDays	Number of days between hatching date and the 1 January in that particular year
Nesting	Nesting	Whether female nested or not in a particular year (0 = no; 1 = yes)

**Table 2** Summary statistics for the reproductive traits used to estimate variance components

	n	Mean $\pm$ SE	Range
ClSize (eggs)	190	43.36 $\pm$ 0.68	23–68
NoViable (eggs)	190	39.47 $\pm$ 0.78	3–68
NoHatch (hatchlings)	190	31.25 $\pm$ 0.83	0–61
HatchR	190	0.72 $\pm$ 0.02	0–1.00
AvSVL (mm)	147	141.7 $\pm$ 0.39	126–152
HDays (days)	186	85.05 $\pm$ 2.14	25–175
Nesting (0/1)	229	0.83 <sup>a</sup>	0–1

<sup>a</sup>Frequency of nesting successes.

of sub-embryonic fluid. This fluid is detectable as a floating mass on top of the yolk when the eggs are moved from side to side. If the clutch has been laid more than 24 h before collection, the beginning of the opaque band provides a more precise indication of a fertile egg and also of the correct 'upright' orientation. The fertile eggs from a clutch are artificially incubated at 32°C in a relative humidity between approximately 90% and 95%. Although crocodilians exhibit temperature-dependent sex determination and 32°C produces mostly males in *C. porosus* (Lang & Andrews 1994), the main reason for incubating at 32°C is to maximize embryo survival (Richardson *et al.* 2002).

Table 1 presents a description of the traits recorded between 1994 and 2002. Descriptive statistics for each trait are given in Table 2. A second data set was constructed for the trait Nesting. This data set consisted of binary data indicating whether a female nested in a particular year or not.

### Statistical methods

The objective of this study was to estimate phenotypic parameters including repeatabilities (upper bounds for heritability) for reproductive traits in

saltwater crocodiles. Using restricted maximum likelihood (REML), appropriate univariate models for each trait were established before combining the traits into a multi-trait analysis for (co)variance component estimation. Repeatability for whether a female nested or not each year (nesting) was estimated using the generalized linear mixed model (GLMM).

### Linear models

Univariate REML analyses were conducted in GenStat 6, version 6.1 (2002) for all traits, except frequency of nesting. The following was the initial model evaluated for all traits

$$Y_{ijklm} = \mu + \beta_L EL_{jk} + \beta_W EW_{jk} + Year_k + Pen_l + Coll_m + Pair_j + \varepsilon_{ijklm}$$

where  $Y_{ijklm}$  is an observation on either ClSize, NoViable, NoHatch, HatchR, AvSVL or HDays;  $\mu$  = the overall mean;  $EL_{jk}$  and  $EW_{jk}$  are the average egg lengths and egg widths of a random sample of 10 eggs for the clutch from the  $j$ th pair in the  $k$ th year (used as a proxy for female age);  $\beta_L$  and  $\beta_W$  are the regression coefficients associated with EL and EW respectively;  $Year_k$  is the fixed effect of the  $k$ th year ( $k = 1994, \dots, 2002$ );  $Pen_l$  is the fixed effect for the breeder environments, i.e. B-pens or UB-pens ( $l = 1, 2$ );  $Coll_m$  (Collected) is the number of days between oviposition and collection ( $m = 0, 1, 2, 3, 5, 10$ ) (all traits except ClSize and HDays);  $Pair_j$  is the random effect of pair [assumed  $N(0, \sigma_{Pair}^2)$ ]; and  $\varepsilon_{ijklm}$  is the random residual effect [assumed  $N(0, \sigma_e^2)$ ]. A 5% significance level was chosen to evaluate explanatory variables by backward elimination. The subsequent univariate models were then combined for multi-trait analysis using ASReml (version 1.10, 2003). Again, fixed effects were omitted from the multivariate model if  $p > 0.05$  using backward elimination.

Repeatability was defined as:

$$\text{Rep} = \frac{\sigma_{\text{Pair}}^2}{\sigma_{\text{Pair}}^2 + \sigma_e^2}$$

where  $\sigma_{\text{Pair}}^2$  and  $\sigma_e^2$  are the estimated pair and residual variance components respectively. The phenotypic correlations between two traits were estimated using standard equations (Searle 1961). Phenotypic standard deviations ( $\sigma_p$ ) were estimated using  $\sqrt{\sigma_{\text{Pair}}^2 + \sigma_e^2}$  as defined by Gregory *et al.* (1995). Note that, because the numerator of repeatability includes both additive genetic and permanent environmental variances, the heritability of a trait will always be less than or equal to the repeatability (Falconer & Mackay 1996).

### Binomial model

The trait Nesting was modelled using a GLMM in ASReml. The trait was binomial because the animal either nested (1) in a particular year or did not (0), and was modelled as

$$\log\left(\frac{P_{jklm}}{1 - P_{jklm}}\right) = \mu + \text{Year}_k + \text{Pen}_l + \beta_m \text{SOI}_k^{(m)} + \text{Pair}_j$$

where  $P_{jklm}$  is the probability of the female nesting, and  $\mu$ ,  $\text{Year}_k$  and  $\text{Pen}_l$  are fixed effects as described above. The southern oscillation index (SOI) is a measure of the cyclic pattern of air pressure movement across the Pacific Ocean used to predict the onset of the monsoon season in northern Australia. Previous studies have reported the SOI of certain months prior to the breeding season in a particular year to affect the degree and timing of reproductive effort (Webb *et al.* 1990 – average June–July SOI; McClure & Mayer 2001 – August SOI). For this study,  $\text{SOI}_k^{(m)}$  is the southern oscillation index for month  $m$  in the  $k$ th year with  $m$  being either June, July, August, average of June and July or average of July and August. These SOI measures were fitted in separate models to ascertain significance. So  $\beta_m$  is the regression coefficient of the corresponding SOI measure. SOI data were obtained for each year from the Australian Bureau of Meteorology website (<http://www.bom.gov.au/climate/current/soihtml1.shtml>; accessed 9 September 2003). Separate models were used to evaluate the significance of each month's SOI within year. As in the linear model analysis,  $\text{Pair}_j$  was specified as a random effect [assumed  $N(0, \sigma_{\text{Pair}}^2)$ ]. This trait could not be included in the multivariate model due to confounding with other traits. That is, when an animal was coded as

not having nested in a particular year (0), the other traits of interest were considered as missing values.

Repeatability for nesting probability was calculated on the unobserved scale using

$$\text{Rep} = \frac{\sigma_{\text{Pair}}^2}{\sigma_{\text{Pair}}^2 + \phi(\pi^2/3)}$$

where  $\sigma_{\text{Pair}}^2$  is the pair variance component and  $\phi$  is the dispersion parameter included to manage any non-binomial variation.

## Results

### Univariate models

The terms found to be significant for each reproductive trait from univariate modelling are shown in Table 3 (those that have the superscript 'M' remained significant in the multivariate model also). The random genetic effect, Pair, was highly significant in all models.

As mentioned before, with the exception of one pair, adult age was unknown. This resulted in the inability to adjust for age and/or parity during the modelling process. Crocodiles exhibit non-determinant growth, i.e. they continue to grow throughout their life, although slowing down as the animal gets older (Thorbjarnarson 1996). Therefore, female size is related to female age. It is not practical to routinely measure or weigh adult female crocodiles. However, crocodilian reproductive biology studies have shown clear allometric trends between

**Table 3** Significant terms for the reproductive traits from univariate REML modelling

Response	Fixed terms					Random Pair
	EL	EW	Pen	Year	Coll	
ClSize	***	***	**	–	NA	*** <sup>M</sup>
NoViable	**	***	***	–	–	*** <sup>M</sup>
NoHatch	**	**	***	–	***	*** <sup>M</sup>
HatchR	–	–	–	–	***	*** <sup>M</sup>
AvSVL	*** <sup>M</sup>	–	–	*** <sup>M</sup>	–	*** <sup>M</sup>
HDays	NA	NA	–	–	NA	*** <sup>M</sup>
Nesting	NA	NA	–	***	NA	***

The fixed terms evaluated were egg length (EL), egg width (EW), breeder pen type (Pen), Year and Number of days collected after oviposition (Coll). Levels of significance are shown as  $0.001 < p \leq 0.05$  (\*\*) and  $p < 0.001$  (\*\*\*). A dash (–) indicates that the term was not significant ( $p > 0.05$ ), whilst NA specifies terms that were not applicable to that trait and were therefore not included in the initial model. Terms significant with the multi-trait REML model indicated with superscript M. Nesting was not included in the multi-trait analysis because of confounding with the other traits.

**Table 4** Regression coefficients for egg length (EL) and egg width (EW) produced from univariate REML analyses

Response	Egg length ( $\pm$ SE)	Egg width ( $\pm$ SE)
ClSize	-1.41 (0.29)	2.01 (0.41)
NoViable	-1.09 (0.36)	2.37 (0.52)
NoHatch	-1.03 (0.38)	1.81 (0.57)
AvSVL	1.00 (0.11)	NA

Egg width was not significant in the AvSVL univariate model, indicated by NA.

female size, clutch size and egg dimensions (Webb *et al.* 1983; Thorbjarnarson 1996). Utilizing this information, egg dimensions (egg length and egg width) were used as proxies for adjusting for female age effects in the reproductive traits under investigation. With the exception of HatchR and HDays, egg length (EL) was a significant predictor for all models. For the traits ClSize, NoViable and NoHatch, egg width (EW) was also significant in conjunction with EL. Regression coefficients for EL and EW predicted from the univariate analyses of these traits are presented in Table 4.

Breeder pen type also had a significant effect on the traits of ClSize, NoViable and NoHatch. Compared with the B-pens, the UB-pens produced clutches with an average of 4.97 more eggs per clutch. Furthermore, an additional 7.93 eggs per clutch were viable and an average of 8.36 additional hatchlings per clutch were produced. These results appear to be a cumulative across the reproductive characters.

The day of collection (Coll) after oviposition greatly affected the embryo survival rate and the overall number of live, healthy hatchlings (NoHatch). The majority of eggs were collected on day 0 ( $n = 142$  nests) with 20, 10, 3, 1, 1 nests being collected on days 1, 2, 3, 5 and 10, respectively. The day of collection was not recorded for 13 clutches.

**Table 5** Estimates of repeatability (bold on diagonal) and phenotypic correlations (below diagonal) with their approximate standard errors in parenthesis below each estimate for saltwater crocodile reproductive traits

	ClSize	NoViable	NoHatch	HatchR	AvSVL	HDays	Nesting
ClSize	<b>0.68 (0.02)</b>						
NoViable	0.86 (0.01)	<b>0.55 (0.03)</b>					
NoHatch	0.54 (0.03)	0.73 (0.02)	<b>0.34 (0.02)</b>				
HatchR	-0.08 (0.04)	0.27 (0.04)	0.78 (0.02)	<b>0.24 (0.02)</b>			
AvSVL	-0.15 (0.04)	-0.06 (0.05)	0.15 (0.05)	0.30 (0.05)	<b>0.57 (0.03)</b>		
HDays	-0.13 (0.03)	-0.04 (0.03)	0.03 (0.04)	0.13 (0.04)	0.10 (0.04)	<b>0.68 (0.02)</b>	
Nesting	—	—	—	—	—	—	<b>0.58<sup>a</sup></b>
$\sigma_P$	9.36	10.87	11.56	0.22	4.29	28.39	—

<sup>a</sup>Repeatability on the underlying scale. Phenotypic standard deviations ( $\sigma_P$ ) are also presented for the measurement-variable traits.

### Multi-trait model and parameter estimates

A multivariate analysis was undertaken with ASReml using the explanatory variables identified as being significant for each trait in their respective univariate models. Note that using this multivariate formulation, ASReml allows a separate set of explanatory variables to be specified for each trait. Those explanatory variables that remained significant at the 5% level are indicated by the superscript 'M' in Table 3.

Repeatability and phenotypic correlation estimates are shown in Table 5. Repeatability estimates are in bold on the diagonal, whilst phenotypic correlations are below the diagonal. The repeatability estimates were high and ranged from 0.24 (HatchR) to 0.68 (ClSize and HDays). Phenotypic correlations ranged from negligible (0.03: NoViable and HDays) to high (0.86: ClSize and NoViable) between the various traits.

### Binomial model and repeatability

The binary trait Nesting had significant year and pair effects. The southern oscillation index (SOI) values for the months of interest were all non-significant. Because this trait was not included in the multivariate model, the univariate GLMM variance component estimates were used to determine repeatability. The pair residual component was 2.49 with a dispersion parameter of 0.56, indicating less variation than expected under a binomial model using a logit-link function. Repeatability on the underlying scale for a female nesting was calculated to be 0.58.

### Discussion

Repeatability estimates set upper limits to heritability (Falconer & Mackay 1996). The estimates of repeatability for reproductive characters in the saltwater

crocodile were high compared with estimates reported in other species (pigs: Kerr & Cameron 1995; Serenius *et al.* 2003; rabbits: Ayyat *et al.* 1995), although the phenotypic correlations were similar to those reported in the other industries. In addition, the phenotypic correlations and non-genetic factors of crocodile reproduction traits presented in this study concur with the results of published biological studies (Webb *et al.* 1983; Ferguson 1985; Deeming & Ferguson 1990; Thorbjarnarson 1994, 1996).

#### Accounting for female age using proxies

The ages of only one female and male used in this study were known. Both were captive-raised, with the female being bred at the Janamba Croc Farm, whilst the male was from a wild-harvested clutch of eggs. The pair first nested when the female was six and the male ten years of age. The first clutch this pair produced (in 1998) consisted of 35 small eggs, in which 25 were infertile and the other 10 died during incubation. For the succeeding three years, clutch size varied increasing to 50, 52 and 46 in the years 1999, 2000 and 2001, respectively, and all are larger than the average clutch size reported for this entire data set (43.36; Table 2). In the same years 1999–2000, the number of hatchlings produced was 14, 29 and 27, respectively, which is slightly below the farm average (31.25; Table 2) although expected to gradually increase with maturity.

Unfortunately, the inability to account for female age could have compromised the estimates presented herein. The relationships between female size (related to age) and different aspects of reproductive output have been well documented (Thorbjarnarson 1996). A clutch characteristic demonstrated by Deeming & Ferguson (1990) in the American alligator (*Alligator mississippiensis*) was more uniform mean egg widths between clutches than mean egg lengths, possibly indicating an oviducal limitation on egg width that does not affect length. In another study, Thorbjarnarson (1994) reported in *Caiman crocodilus* an inverse relationship between egg length and clutch size, suggesting limitations on linear egg placement within the oviduct of smaller animals (Ford & Seigel 1989); i.e. as the female continues to grow older, its pelvic canal diameter increases, determining the resulting egg and clutch sizes. Similar trends have also been shown in the poultry (Bell 2002) and aquaculture (Guo-Sheng *et al.* 2002) industries.

Using this information, egg length and width measurements were used in an attempt to account

for some clutch variation caused by female age. As can be seen from the regression coefficients in Table 4, as egg length increased by 1 mm, the reproductive characters (ClSize, NoViable and NoHatch) decreased, similar to the trend shown in *C. crocodilus* (Thorbjarnarson 1994). Contrary to this, as egg width increases by 1 mm, the reproductive characters increase. This was expected in accordance with the results presented by Deeming & Ferguson (1990); i.e. if egg width is restricted by oviducal limitations, which in turn are restricted by female size (and age), then her ability to produce more eggs of a larger size will increase as the female grows (and ages).

#### Relationships between the 'egg' traits

The estimates of phenotypic correlations between clutch size, the number of viable eggs and the number of hatchlings produced were positive and high (Table 5). In contrast, the phenotypic correlations between hatchability and ClSize, NoViable and NoHatch were  $-0.08$ ,  $0.27$  and  $0.78$  respectively.

The type of pen enclosure that the breeders are maintained in had a significant effect. The UB-pens produced a higher average ClSize, NoViable and NoHatch compared with the B-pens. Possible explanations could include reduced exposure to male aggression due to a larger pen size, and the ability for crocodiles in the UB-pens to thermoregulate and maintain optimal *in utero* conditions for the embryos both prior to and during gestation.

The inability to determine genetic correlations from the information provided by this data set questions the validity of using NoHatch and/or HatchR as the determining trait for the number of offspring produced from each clutch. That is, the high, positive phenotypic correlation estimates obtained between NoHatch and ClSize could just be a numerical consequence of an increased clutch size resulting in more embryos surviving. However, using the trait HatchR instead of NoHatch creates modelling complexities, particularly with interpretation of results. That is, because the traits ClSize and NoViable have a large range of values (as shown in Table 2), from the perspective of a farm enterprise, a 50% hatch rate from a clutch of 50 eggs is better than 100% from 10 eggs. This implies that there is an optimum between NoHatch and HatchR. However, many of these issues can not be further dealt with until a pedigree structure is available to estimate the relevant genetic parameters.

### Relationship between hatchling size and egg traits

In general, larger crocodilian eggs produce larger offspring (Ferguson 1985). The regression coefficient of egg length from the univariate analysis on average snout-vent length was 1.00 mm/mm EL (SE 0.11 mm; Table 4), which concurs with Ferguson (1985). The phenotypic correlations between AvSVL and the egg traits (ClSize, NoViable, NoHatch and HatchR) were not consistent (Table 5). The correlation with ClSize was  $-0.15$ , indicating that as clutch size increases, the hatchling size decreases. This appears to be valid because as egg length increases, clutch size decreases whilst hatchling size increases. AvSVL has almost a zero correlation with NoViable ( $-0.06$ ), whilst there is a small, positive relationship with number that hatch ( $0.15$ ). There was a moderate correlation ( $0.30$ ) between average SVL and hatchability.

### Relationship between time of nesting and other traits

For time of nesting (as indicated by when the juveniles hatched, or HDays), a small, negative correlation estimate was found with clutch size ( $-0.13$ ), whilst the same magnitude estimate of opposite sign was found using hatchability ( $0.13$ ). This may be indicative of the large effect clutch size had in deriving the trait hatchability. A small, positive correlation was also found with AvSVL ( $0.10$ ). However, the correlations between HDays with NoViable and NoHatch were non-significant and almost zero ( $-0.04$  and  $0.03$  respectively).

The repeatability estimated for time of nesting was  $0.68$ , indicating that females have a tendency to lay at approximately the same time each year. This concurs with the result reported by McClure & Mayer (2001) whose study was similar in design and duration (9 years) to this study. Timing of nesting has been reported to be affected by social dominance hierarchies in American alligators, where the larger, more dominant females mate and nest first (Ferguson & Joanen 1983; Ferguson 1985). However, this study, and that of McClure & Mayer (2001), do not support this explanation because the crocodiles were in uninitiated pens where such social interactions do not exist.

Contrary to the study of wild populations conducted by Webb *et al.* (1983), this study showed that there is a slight, negative relationship between clutch size and time of nesting under farm conditions. This again confirms the results of McClure & Mayer (2001). However, McClure & Mayer (2001)

also reported that higher hatch rates were achieved with earlier nesting females. In contrast, a non-significant relationship between NoHatch and time of nesting was found in this study [phenotypic correlation  $0.03$  (SE  $0.04$ ); Table 5]. Although non-significant, the clutches that are laid later produce slightly larger hatchlings as indicated by the average snout-vent length phenotypic correlation of  $0.10$  (SE  $0.04$ ; Table 5). However, in terms of improving production efficiency, the size of the offspring at hatchling has no real relevance to post-hatching growth rates (see Isberg *et al.* 2005).

### Nesting success

McClure & Mayer (2001) and Webb *et al.* (1990) reported significant relationships between whether a female nested in a particular year and the SOI for a particular month. The degree and timing of nesting within the wet-season is closely associated with the climatic conditions prevailing late in the dry season. Low water levels between August and October, combined with high temperature conditions, are generally associated with a reduced nesting effort. In contrast, high water levels and cool conditions result in maximal nesting activity. More specifically, late dry-season rains and intense periods of rain throughout the wet season are the environmental stimuli required for courtship and mating (Webb & Manolis 1989). Because of this interrelationship between water level, rain and temperature, reproductive output in the wild can be predicted as much as 7–8 months prior to the nesting season (Webb *et al.* 1987).

Webb *et al.* (1990) reported a significant relationship between the degree of nesting and the average SOI for June and July, whilst McClure & Mayer (2001) reported that August was a more appropriate predictor for their data. The SOIs used in this study (June to September, and the averages for June–July and July–September) were all non-significant. In contrast, the fixed effect, Year, was highly significant in the model. An explanation could be that Year is a term that encompasses not only air pressures and water heights (SOI), but also air temperature, relative humidity and other climatic factors. The random factor, Pair, accounted for a considerable amount of variation that McClure & Mayer (2001) did not attempt to account for in their modelling procedure (ANOVA).

### Conclusions

Repeatabilities for economically important reproductive traits were estimated to set upper limits for

heritabilities with notably high estimates for all traits. Their implementation in a genetic improvement programme must be conservative because heritability estimates for reproductive traits are usually substantially lower than these estimates of repeatability, which provide only a starting point for designing selection for future breeding animals. In addition, these results reveal that the design of crocodile breeding pens is important when considering reproductive success.

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