

Reproductive trade-offs in *Caiman crocodilus crocodilus* and *Caiman crocodilus yacare*: implications for size-related management quotas

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Management strategies for crocodylians often include size-selective quotas designed to protect breeding females. However, little is known about among- and within-population variation in size and fecundity in crocodylians. Life-history theory predicts trade-offs between clutch size and egg size. Larger females usually have larger clutch sizes, and if they also produce larger eggs their contribution to reproductive effort may be greater than the number of eggs they produce. We studied the relationships among female size and clutch characteristics for an Amazonian population of *Caiman crocodilus crocodilus* between 2001 and 2007, and a Pantanal population of *Caiman crocodilus yacare* in 1996. Females in the Amazonian population were smaller, and showed significant differences from the Pantanal population for some relationships. Eggs lost weight during incubation in the Amazonian population but not in the Pantanal population. Despite these differences, the effect of egg size accounted for about one quarter of the total effect of female mass on clutch mass in both populations. Size-selective quotas should take into account that large females produce both more and larger eggs than do small females. However, size distributions of breeding females vary greatly among populations and legal size limits will be more effective if based on data from local populations.

Key words: breeding females, *Caiman crocodilus*, life-history, reproduction

INTRODUCTION

Ectothermic vertebrates frequently reproduce at sizes much smaller than those that they will eventually attain (Stamps et al., 1998), and crocodylians are no exception (Jacobsen & Kushlan, 1989). This has important consequences for wildlife management strategies, which are frequently based on size-selective quotas (Caughley & Sinclair, 1994), and has implications for life-history theory. Cole (1954) showed that the production of a single extra offspring by a semelparous species has the same numeric consequences as immortality in an iteroparous species. These extremes illustrate the trade-off implicit in the reproductive strategy of any species. Increases in size or longevity imply increased investment by the mother, and hence a reduction in the number of offspring.

Iteroparous organisms could potentially adjust their reproductive output to the energy resources available each year (Ballinger, 1983; Seigel & Fitch, 1985; Turner, 1977), but there is no evidence that crocodylians do this. The species that have been studied appear to adjust the interval between clutches rather than the number of eggs per clutch in response to resource availability (Joanen & McNease, 1987, 1989; Webb & Smith, 1987). This means that clutch mass may be limited by the space available within the female's body cavity, though some species accumulate energy reserves that will later be mobilized for reproduction, and this can be influenced by food avail-

ability over several years (Shine, 2005). For some species of crocodylians, it is known that clutch size is related to female size (Cott, 1961; Graham, 1968; Hall & Johnson, 1987; Thorbjarnarson & Hernández, 1993; Thorbjarnarson, 1994; Campos & Magnusson, 1995) and indirectly to female age (Joanen & McNease, 1987).

Female reptiles presumably fill their body cavities with eggs to some optimal degree (Qualls & Shine, 1995). However, this involves another trade-off. Larger females could invest in more eggs or invest in larger eggs. Larger eggs produce larger hatchlings in *Alligator mississippiensis* (Deitz & Hines, 1980) and *Caiman crocodilus yacare* (Campos & Magnusson, 1995), and larger hatchling *Crocodylus porosus* have higher survivorship than smaller hatchlings (Messel & Vorlice, 1989).

Many monitoring and harvest programmes for crocodylians are based on night-time surveys that estimate sizes of individuals encountered (Magnusson, 1983), and size distributions are often converted to categories of life stages, such as "hatchling", "juvenile" and "adult" (e.g. Brazaitis et al., 1996). However, interpretation of size distributions is difficult because it is not possible to distinguish the sex of animals seen, and there is strong sexual dimorphism in size in crocodylians. In general, it is not possible to distinguish subadult males from adult females. Monitoring of nests is much more cost effective in some situations (Hines & Abercrombie, 1987; Hollands, 1987), and focuses directly on the breeding segment of the population. Where females associated with nests can

be measured, or there is a strong relationship between clutch characteristics and female size, nest surveys may allow inferences about the size structure of the breeding population.

Management programmes in the Venezuelan llanos target *C. c. crocodilus* larger than 180 cm total length – about 90 cm snout–vent length (SVL) – which are assumed to be largely or exclusively males (Seijas, 1984; Velasco & De Sola, 1999), and the same classification has been used in Bolivia for *C. c. yacare* (Querejazu & Effen, 1999). However, the average size of reproductive individuals is much smaller in other regions in Venezuela (Gorzula, 1987). Micucci & Waller (1995) considered that *Caiman latirostris* and *C. c. yacare* over 170 cm total length (about 85 cm SVL) in Argentina were exclusively males.

Coutinho et al. (2001) only found mature ovaries with advanced vitellogenic follicles in female *C. c. yacare* larger than 70 cm SVL, but the minimum size for reproduction in female *C. c. crocodilus* is generally given as 60 cm SVL (Staton & Dixon, 1977; Thorbjarnarson, 1994; Magnusson & Sanaiotti, 1995). Thorbjarnarson (1994) did not find evidence for a trade-off between egg size and clutch size, but the other studies did not address this question.

If larger females are more fecund and produce larger offspring, management strategies that target large individuals may not always be the best strategy, even if females are a small proportion of the harvest. In this study, we investigated the relative contributions of increase in egg number and increase in egg size to the reproductive effort of populations of *C. c. crocodilus* and *C. c. yacare* as indexed by total clutch mass. *Caiman crocodilus* is one of the most widespread species of cayman, and is subject to legal size-selective harvesting in Brazil (Governo do Estado do Amazonas, 2006) and Venezuela (Velasco et al., 2003).

MATERIALS AND METHODS

Study area

The first part of the study was conducted on Campo Dora and Nhumirim Ranches in an area of intermittent rivers in the Central Pantanal (18°55'S and 56°39'W; elevation 60 m), Mato Grosso do Sul State, Brazil. The study site has been described by Campos & Magnusson (1995) and Campos et al. (2006). Nests of *C. c. yacare* around water bodies were located on horseback or on foot in January and February 1996. The second part of the study was conducted around Cururu Lake, on the floodplain of the Solimões River (03°34'S and 60°40'W; elevation 80 m), Amazonas State, Brazil. We searched on foot for nests of *C. c. crocodilus* in the seasonally flooded forest around the lake and small streams, at distances 15–20 m from water, in October and November of 2001, 2002, 2005, 2006 and 2007.

Egg and female biometry

At the Amazonian site, eggs from each nest were counted, but due to time restraints, only 10 eggs in each nest were measured in surveys between 2001 and 2006. All eggs in each nest were measured at the Pantanal site and at the

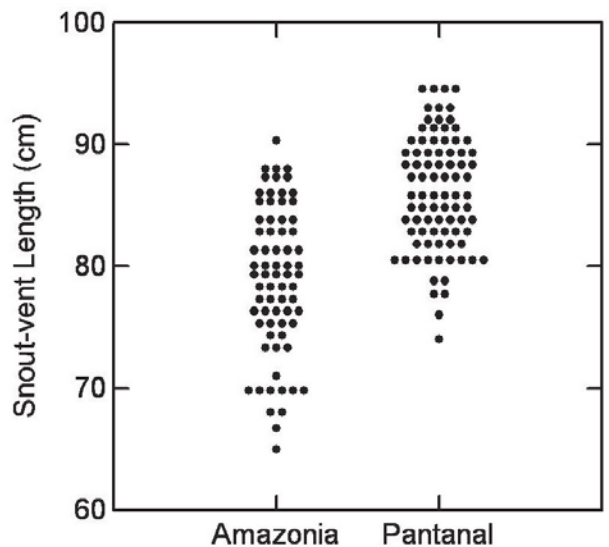


Fig. 1. Snout–vent lengths of females attending nests in an Amazonian (left) and a Pantanal (right) population of *Caiman crocodilus*.

Amazonian site in 2007. Egg length and width were measured to the nearest 0.1 mm with vernier callipers to the nearest 0.1 mm and eggs were weighed with a spring balance to the nearest 1 g. Females attending nests were captured and their snout–vent length to the posterior edge of the cloaca (SVL) measured with a measuring tape (accurate to 0.5 cm). They were weighed with a spring balance (accurate to 0.5 kg).

One egg from each nest was opened and the curled length (Crawshaw, 1987) of the embryo measured with a vernier caliper to the nearest mm. Embryo length was used as an index of nest age in analyses.

Egg volume (EV) was estimated from the length (L) and width (W) of eggs with the equation for an ellipsoid:

$$EV = 4/3 \times L/2 \times (W/2)^2.$$

Use of this formula may slightly underestimate egg volume if eggs are more elongate or have bicone values greater than a pure ellipse, but estimates will be linearly related to true volume (Maritz & Douglas, 1994).

Path analyses

Simple or multiple least squares regressions were used for inferential tests. However, female size has only indirect effects on clutch mass through egg size and number of eggs. The relative effects of mean egg mass and clutch size on clutch mass were evaluated through path analyses (King, 1993). Only simple path analyses were used rather than structural equation modelling (Grace & Pugsek, 1998) because the final dependent variable (clutch mass) was constructed mathematically from mean egg size and clutch size in some years, and the predictor variables explain over 99% of the variation in clutch mass. Analyses of residual variation are meaningless in this context. Evaluation of the consistency of the results was based on the similarity in the magnitude of the indirect effects estimated in the two independent populations of caymans.

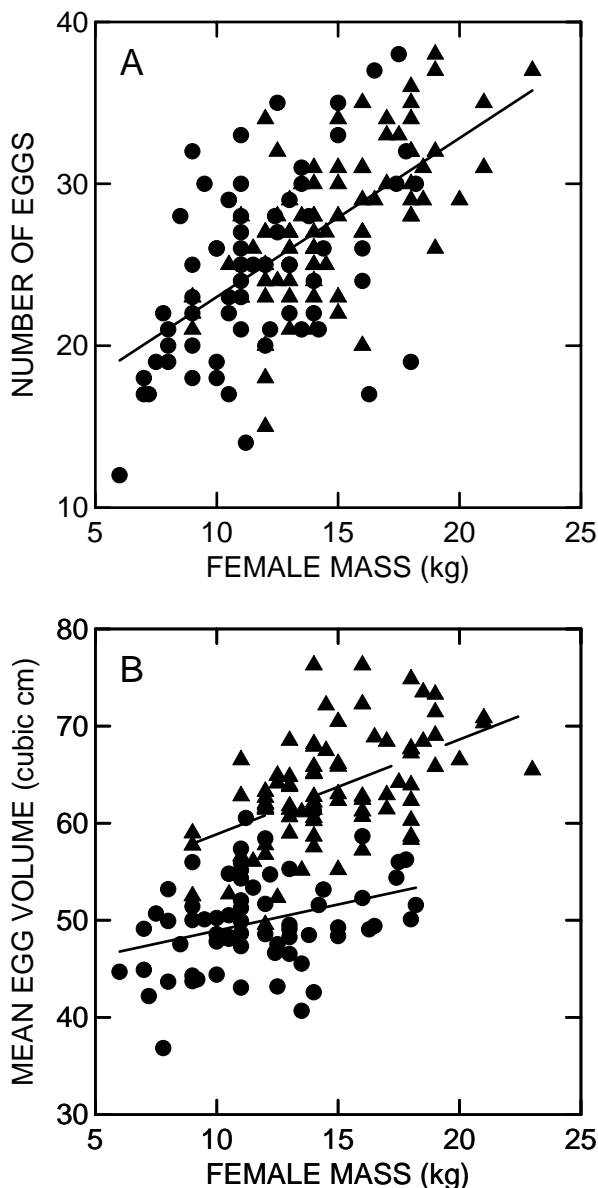


Fig. 2. Relationship between (A) clutch size and female mass and (B) egg volume and female mass, for individuals from an Amazonian (circles) and a Pantanal (triangles) population of *Caiman crocodilus*.

RESULTS

Size of reproductive females

The mean size of female caymans captured near nests was much greater in the Pantanal than at the Amazonian site (Fig. 1). Only one of 71 females attending nests at the Amazonian site exceeded 90 cm SVL (about 180 cm total length). In contrast, individuals larger than 90 cm SVL represented 22.4% of the 85 females attending nests in the Pantanal. Twenty percent of females attending nests at the Amazonian site were smaller than the smallest breeding female found in the Pantanal.

Effects of female mass on clutch characteristics

There was no significant effect of study area or interaction between study area and female mass on number of

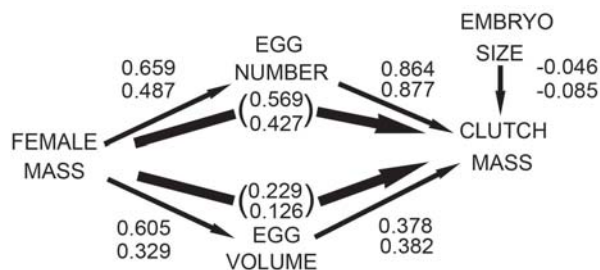


Fig. 3. Path diagram illustrating the indirect effects of female mass on clutch mass. Numbers represent path coefficients, which are derived from standardized regression coefficients and indicate the expected magnitude of an effect indicated by the arrow. Path coefficients indicate the number of standard deviations in the dependent variable expected for a one standard deviation increase in the predictor variable. Upper numbers in each pair indicate values for the Pantanal population and lower numbers indicate values for the Amazonian population. Numbers within parentheses in internal arrows indicate indirect effects calculated by multiplying coefficients along sequential arrows.

eggs per nest ($P=0.56$ and $P=0.57$ respectively). Therefore, data for the two areas were combined to evaluate the relationship between female mass (FM) and number of eggs (NE). There was a positive (Fig. 2A) relationship between the two variables ($NE = 13.2 + 0.981 \times FM$, $n=153$, $r^2=0.38$, $F=93.7$, $P<0.001$). There was some evidence for an interaction between study area and female mass on mean egg volume per nest ($P=0.097$), and there was a significant effect of the interaction between study site and number of eggs on clutch mass ($P<0.001$). Both indicate that the relationship between female size and mean egg size differs between the two areas, and predictions for management generally will be made within rather than between areas, so relationships involving mean egg volume and clutch mass were analysed separately for each area.

There was a positive (Fig. 2B) relationship between female mass and mean egg volume (EV) in both the Amazonian ($EV = 43.6 + 0.538 \times FM$, $n=68$, $r^2=0.11$, $F=93.7$, $P=0.006$) and Pantanal populations ($EV=49.1 + 0.975 \times FM$, $n=84$, $r^2=0.27$, $F=29.8$, $P<0.001$), though the relationship was weaker in the Amazonian population. In general, Amazonian females produced smaller eggs for a given female size.

Number of eggs in the clutch ($P<0.001$), mean egg volume ($P<0.001$) and embryo size, ES ($P=0.021$) were related to clutch mass (CM) in the Amazonian population ($CM = -1176 + 51.80 \times NE + 25.34 \times EV - 4.49 \times ES$, $n=53$, $r^2=0.94$, $F=254.1$, $P<0.001$). In the Pantanal population, clutch size ($P<0.001$) and mean egg volume ($P<0.001$), but not embryo size ($P=0.153$), were significantly related to clutch mass ($CM = -1533 + 69.80 \times NE + 24.96 \times EV - 3.219 \times ES$, $n=66$, $r^2=0.94$, $F=308.4$, $P<0.001$). Crocodilian eggs have hard shells, and therefore fixed volume for most of the incubation period. Therefore, we assume that the negative

relationship between clutch mass and embryo size in the Amazonian population was due to water loss.

Female mass was more reliably predictable from clutch characteristics (number of eggs and mean egg volume) in the Pantanal population ($FM = -10.5 + 0.38 \times NE + 0.23 \times EV$; $n=84$; $r^2=0.62$; $F=66.7$; $P<0.001$) than in the Amazonian population ($FM = -3.63 + 0.25 \times NE + 0.18 \times EV$; $n=67$; $r^2=0.33$; $F=15.4$; $P<0.001$). Despite the statistically significant effect of embryo size in the Amazonian population, female mass could be predicted from clutch mass in the Pantanal ($FM = -3.08 + 0.006 \times CM$; $n=83$; $r^2=0.61$; $F=128.2$; $P<0.001$) and in the Amazonian population ($FM = 4.81 + 0.25 \times NE + 0.005 \times CM$; $n=67$; $r^2=0.35$; $F=34.4$; $P<0.001$).

Although there were statistically different relationships for some variables, path analysis indicated similar effect sizes for most variables in the two populations (Fig. 3). Female mass explained about 61% of the variability in clutch mass in the Pantanal population, but only about 35% for the Amazonian population. The indirect effect of female mass through egg volume accounted for 23% of the total effect size of female mass on clutch size in the Amazonian population, and 29% for the Pantanal population.

DISCUSSION

The size distributions of females in the two populations we studied were very different. Some authors consider *C. c. crocodilus* and *C. c. yacare* to be different species (Busack & Pandya, 2001). However, the two forms intergrade smoothly along a cline of over 1000 km in the Madeira River and its tributaries (Brazaitis et al., 1998), and large differences in size distributions among populations have been recorded for both *C. c. crocodilus* (Gorzula, 1987) and *C. c. yacare* (Campos & Magnusson, 1995). Adoption of a lower size limit of 180 cm total length (about 90 cm SVL), as used in the Venezuelan llanos (Velasco et al., 2003), would protect most of the females in the Amazonian population we studied. However, 22% of the breeding females in the Pantanal population were larger than this limit, and they produced about 26% of the eggs. The same considerations apply to upper size limits. An upper size limit of 75 cm SVL would protect almost all of the females in the Pantanal population we studied, but would expose 27% of females in the Amazonian population to hunting. When size limits are justified on the basis of protecting breeding females, they should be based on the size distribution of females in the local population, and not extrapolated from data collected in other regions.

Conventional spotlight surveys are of limited utility in monitoring changes in the size distribution of breeding female crocodylians because it is usually impossible to distinguish juvenile males from adult females. Estimates of sizes in spotlight surveys can be used to place animals seen in broad categories, such as hatchling, intermediate and large, but they are very imprecise within these categories. This study has shown that the about 60% of the variance in nesting female size can be predicted from clutch characteristics in the Pantanal, and this level of precision is far greater than can be expected for spotlight

counts for this demographic segment. Monitoring programmes that rely on nest surveys may be able to use data on clutch characteristics to make inferences about the size structure of the breeding female population. However, clutch characteristics only accounted for about 35% of the variance in female size for the Amazonian population, so inferences about sizes of breeding females in this population would be imprecise and might not justify the cost of obtaining the data unless nests are being studied for other reasons.

The results of this study indicate that eggs in the nests of the population of *C. c. crocodilus* we studied lose weight during incubation, and this is probably due to water loss. Caymans in this population nest at the end of the dry season, when river levels are low. In contrast, there was no relationship between embryo development and egg weight in the Pantanal population, where caymans usually start nesting after the start of the wet season. Clutch mass depends on a number of components, some of which may not contribute a fitness advantage to hatchlings, and we do not know whether larger eggs have a higher energy content. However, it could be an advantage to have larger eggs with more water even if larger eggs do not have greater energy content, because dehydration can impose fitness costs if it interferes with development towards the end of incubation. Nest hydration affects hatchling size in turtles (Packard et al., 1987).

Campos & Magnusson (1995) did not find a relationship between mean egg mass and female mass or clutch size for *C. c. yacare*, but that conclusion was based on a small sample. Thorbjarnarson (1994) found statistically significant correlations between female SVL, clutch size and clutch mass, but not between female SVL and egg mass, in *C. c. crocodilus* in Venezuela. The difference between our study and that of Thorbjarnarson (1994) could indicate a difference among populations, but it is possible that the difference is because we used volume as an index of egg size and the Venezuelan study used egg mass, which may vary with incubation period. In this study, we found a significant effect of female size on egg size, and the magnitude of the effect of female size on clutch mass, through its effect on egg size, was similar in both populations we studied (23% and 29% of the total effect size, respectively).

Larger eggs produce larger hatchlings in *C. c. yacare* (Campos & Magnusson, 1995) and *Alligator mississippiensis* (Deitz & Hines, 1980), and larger hatchling *Crocodylus porosus* are more likely to survive than smaller hatchlings (Messel & Vorlicek, 1989). As larger female caymans use space in the body cavity to produce larger eggs that could have been used to produce more eggs, there is presumably a fitness advantage for females that produce larger eggs. Follicle ablation or hormonal manipulation that decrease clutch size result in larger offspring in lizards (Sinervo & Licht, 1991, Sinervo et al., 1992). As the larger eggs are produced only by the largest females, the fitness value of larger eggs is presumably a function of female size, egg number being relatively more important for small females and egg size relatively more important for larger females.

Our results indicate that changes in egg size associated with changes in female size in *C. c. crocodilus* and *C. c. yacare* account for about a quarter of the changes in clutch mass. As larger females produce relatively larger eggs, and hence hatchlings that are probably larger and more likely to survive, establishment of size-selective quotas should take into account the effect on overall reproductive potential, and not just the number of females affected. Hunting larger females may allow smaller female alligators to breed (Hines & Abercrombie, 1987). However, there is no evidence that female caymans inhibit breeding of other females. If females are vulnerable to hunters, in some situations, an upper size limit, rather than a legal minimum size, may be the more appropriate strategy to maintain viable populations in the long term.

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