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EGG RETENTION AND MORTALITY OF GRAVID AND NESTING FEMALE CHAMELEONS (*CHAMAELEO CHAMAELEON*) IN SOUTHERN SPAIN

MA. CARMEN BLÁZQUEZ, CARMEN DÍAZ-PANIAGUA AND JOSÉ A. MATEO

Estación Biológica de Doñana (CSIC), Apdo. 1056, 41080 Seville, Spain

In a year of drought conditions, gravid chameleons showed difficulties at the time of oviposition and made unsuccessful attempts at nesting. Two females died while constructing nests and 10 females retained eggs in the oviduct after oviposition; death was subsequently confirmed for three of the latter. Female chameleons that died whilst laying eggs, or those that retained eggs, were smaller in body length and body mass and were in poorer physical condition than females that survived long after nesting. After depleting their reserves by allocating them to egg production, it is unlikely that some females were able to complete the gravid period in sufficiently good condition to survive the effort of nesting and oviposition,

Key words: *Chamaeleo chamaeleon*, reproduction, egg-retention, nesting, cost, mortality

INTRODUCTION

Investment in reproduction requires the allocation of energy in the development of eggs or offspring to the detriment of other biological processes, such as growth. The cost of reproduction in reptiles has been reviewed by Shine (1980) and Shine & Schwarzkopf (1992), and can involve (1) survival (or mortality) costs that reduce the probability of survival of reproducing organisms (see also Schwarzkopf, 1993); and (2) energy costs, which imply the reduction of future fecundity as a consequence of higher allocation of energy to reproduction rather than growth. Both types of cost may be closely related, as a high energetic expenditure in reproduction may be the cause of mortality in some species, as has been reported for some snakes after giving birth (Madsen & Shine, 1993; Luiselli, Capula & Shine, 1996).

The common chameleon, *Chamaeleo chamaeleon*, is a medium-sized arboreal lizard that is widely distributed in North Africa, the near Orient and several areas of southern Europe (Schleich, Kästle & Kabisch, 1996). Its reproduction is annual, with summer courtship, autumn oviposition, and an incubation period of about 10 months (Bons & Bons, 1960; Blasco, Romero Sánchez & Crespillo, 1985; Cuadrado & Loman, 1999).

In this paper we report on mortality in reproductive female chameleons that we assumed to be related to the investment in reproduction during a period of drought. The reproductive characteristics of female chameleons of the population studied have been described elsewhere (Díaz-Paniagua, Cuadrado, Blázquez & Mateo, submitted), but are summarized here. Female chameleons annually lay a single clutch of 2-40 eggs in an underground nest which they dig at the end of a long tunnel. Clutch size is correlated with maternal size. The comparison of a wet year with a dry year revealed that females made a higher investment in reproduction and suffered a lower mortality rate in the wet year, which was explained as a consequence of the lower availability of food during the dry year. The aim of the present study was to explain the cause of mortality of females by comparing characteristics of surviving and non-surviving individuals.

Correspondence: C. Díaz-Paniagua, Estación Biológica de Doñana (CSIC), Apartado 1056, 41080 Seville, Spain. *E-mail:* paniagua@cica.es

METHODS

Data were collected in a coastal area of southern Spain (in Cádiz province), characterized by semi-abandoned agricultural fields of sandy soil, where dispersed thickets of broom shrub (*Retama monosperma*) or garden trees (*Prunus* spp. and *Myoporum tenuifolius*) are the main arboreal habitat for chameleons. The study was carried out during the autumn of 1995, the fourth year of a prolonged drought in the area. Rainfall during the year from September 1994 to October 1995 was 215 mm, whereas the mean annual rainfall over a 150-year period in this area was 573 mm ±189 mm. During October and November 1995, an intensive search for female chameleons in this area was carried out by three persons walking slowly while inspecting the surrounding habitat. Once chameleons were located, they were measured (snout to vent length, SVL), weighed to the nearest 0.5 g and marked with nail polish spots on their limbs. We recorded information on nesting attempts by females and marked the locations of the nests. Egg retention after nesting attempts was assessed by abdominal palpation.

When possible, we weighed females before oviposition (gravid body mass, GBM) and after nesting (post-nesting body mass, PNM). The relative clutch mass (RCM) was estimated as the ratio of the difference between gravid and post-nesting body mass to post-nesting body mass (RCM = [GBM-PNM]/PNM). For gravid females found recently dead, we considered the mass of all eggs extracted as clutch mass, and their RCM was calculated as clutch mass divided by the body mass of the female without eggs. Of eleven females that we found dead, we only could record biometric data from nine individuals.

We estimated the physical condition of females using the residuals from a linear regression of log body mass (without eggs) on log SVL. For this purpose we included data from females that survived long after their nesting in 1996, a rainy year in which availability of resources appeared to be considerably higher than in 1995. For estimates of RCM and physical condition in live females retaining eggs after oviposition, we made a transformation of PNM by subtracting 1g (the approximate mean egg mass in 1995, Diaz-Paniagua *et al.*, submitted) per egg detected.

For comparisons, 1995 gravid females were categorized as (a) survivors: females whose survival was confirmed at least 30 days after successful egg-laying ($n = 11$); (b) dead females: this group included females that were found dead before or after nesting and for which a cause of death was not evident, i.e. we excluded females killed by predators or vehicles ($n = 11$); and (c) dead and egg-retaining females (n=18): females that were observed to retain eggs in the oviduct after a first oviposition, plus those of the former (b) group.

Comparisons of characteristics of dead and surviving females were made by ANOVA, and Pearson correlation coefficients were used to relate RCM and SVL. Linear regression was calculated for body mass and SVL after logarithmic transformation of the variables.

RESULTS

During the nesting period of chameleons in 1995 we observed 87 females, of which 78 (90%) were confirmed to become gravid.

Nest construction requires a considerable effort by chameleons, as deduced from the time invested in it. On six occasions, we observed females starting and completing nest construction. Females usually started digging in the afternoon (about 1400 GMT) and continued during the next morning, averaging 23.2±2.1 hr (mean±SD) in a successful nesting event. While excavating the tunnel, the female chameleon frequently re-emerged to remove sand. When the tunnel was complete, the female came outside again and entered the tunnel backwards to lay its eggs. The tunnel was then closed by pushing sand into it. The process of nesting was concluded by completely camouflaging the tunnel entrance.

In the study year, we found gravid females making several unsuccessful attempts at nesting before construction of a successful nest. In total, we observed thirty unfinished nesting tunnels (referred to as attempts) and 47 successful nests. Unsuccessful nesting attempts may carry a high energetic cost for females, as females were observed digging for up to six hours, with tunnels as long as 48 cm, without laying. We also observed two females that completed and closed tunnels in which they had not laid eggs, and also recorded two additional empty nests. Some females had severe physical difficulties laying, and made nesting attempts during successive days. One was observed making three successive attempts within a period of 18 days. The same female was found dead 31 days after the first observed attempt, still bearing her clutch. Another two females were found dying during nest construction, one before completing the tunnel, and the other after having laid three eggs and with six eggs still in her oviduct. Of those females for which a successful nesting was confirmed after unsuccessful attempts, one laid her eggs 16 days after the first nesting attempt; another was observed to make an attempt six days before nesting; three females made attempts two days before nesting and one was observed to make an attempt the day before nesting.

TABLE 1. Number of gravid females which were assumed to show difficulties at the time of oviposition.

	Death confirmed	Death not confirmed
Females which were not able to oviposit	7	2
Females retaining eggs after oviposition	3	7
Females dead after ovipositing	1	-

In 10 females, we observed egg retention after a first oviposition (Table 1); three of these females were later found dead, one dying 25 days after the first oviposition. We found no evidence of any female ovipositing twice in the same breeding season.

On one occasion, we observed a female that, instead of starting to dig a new tunnel, continued the construction of a tunnel that had been previously dug and abandoned by another female. Another case of opportunism is illustrated by a gravid female that was observed to lay its eggs in the nest that was being excavated by another female, both females being inside the nest tunnel at the same time.

Comparison of the characteristics of females from the three groups considered (Table 2) revealed that dead females did not differ significantly in SVL or GBM from survivors, but that they had significantly lower PNM (Table 2). Egg-retaining females were significantly smaller in SVL, GBM, and PNM than those surviving: all dead and egg-retaining females did not surpass 20 g body mass (without egg mass), whereas all those surviving ones had a PNM greater than 20 g. A wider range of RCM was observed in dead and egg-retaining females than in surviving females, although the mean values did not differ significantly (Table 2).

TABLE 2. Snout-vent length (mm); gravid body mass (g); Post-nesting body mass (g); and relative clutch mass of female chameleons, grouped into those surviving after nesting, those which died during the nesting season, and those for which egg retention was confirmed (this third group also included the females of the second group). All ANOVA values indicated compared the values of the group indicated with the group of surviving females.

	mean±SD	range	*n*	*F*	*P*
Snout-vent length					
Survivors	102.0±8.1	85-116	11		
Dead	97.7±9.6	87.5-118	9	1.2	NS
Egg-retaining	94.07±8.5	85-118	18	5.79	0.024
Gravid body mass					
Survivors	37.5±9.1	28-56	8		
Dead	29.2±7.2	18.4-42	9	4.39	0.054
Egg-retaining	28.7±6.4	18.4-42	16	6.9	0.016
Post-nesting body mass					
Survivors	24.1±3.7	20-30	8		
Dead	17.2±3.2	11.2-20	8	15.34	0.0016
Egg-retaining	17.9±2.9	11.2-21	14	17.62	0.0005
Relative clutch mass					
Survivors	68.9±12.2%	57.1-86.7	5		
Dead	67.1±26.2%	22.2-110%	8	0.02	NS
Egg-retaining	61.0±28.2%	20-110%	11	0.35	NS

However, we observed that in surviving females RCM was significantly correlated with SVL (r=0.947, P=0.014); this relationship was not significant in the case of dead and egg-retaining females (r_{dead}=0.449, P=0.264; $r_{egg\text{-}retaining}$=0.551, P=0.07). Only in the case of surviving females was GBM significantly correlated with SVL (log GBM = -2.78 + 2.17 log SVL; R^2=0.778).

In the analysis of physical condition, we compared the data of surviving 1996 females, of survivors in 1995 and of dead females in 1995. We found significant differences between the three groups ($F_{2,27}$=6.84, P=0.0039), and an *a posteriori* Duncan Test revealed that the group of dead 1995 females showed poorer condition than the other two groups. The regression of log PNM on log SVL showed a good fit to the data (R^2=0.525). The condition index of dead females and of those surviving from 1995 is shown in Fig. 1.

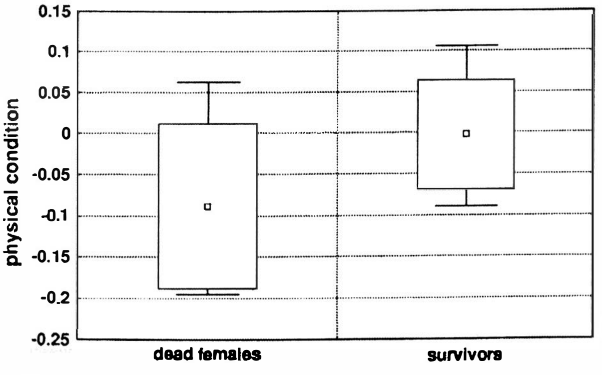

FIG. 1. Mean, standard deviation and range of the physical condition of dead and surviving females in 1995.

DISCUSSION

The unsuccessful nesting attempts observed, and the cases of egg retention after a first oviposition, indicate that some females had difficulties in laying, or even became egg-bound. In birds, excessively large eggs may be a cause of egg-binding and intensive breeding may cause exhaustion in females (Arnall & Keymer, 1975). The high relative clutch mass of chameleons *per se* indicates that females allocate a high energetic investment to reproduction (Díaz-Paniagua *et al.*, submitted), which, because of the enormous clutch, may have a negative effect on maintenance activities, and be detrimental to the female's physical condition. For example, the large volume of eggs may constrain food intake (Bons & Bons, 1960). It is likely that, clutches being too large to be borne, some females concluded their gravid period in such poor condition that they were not able to manage the final effort required in the arduous processes of nesting and oviposition. Furthermore, this effort becomes even greater when they have to perform successive attempts, and may finally conclude in their exhaustion, and difficulty in laying eggs. With such costly nesting processes, it is probable that a portion of females have adopted opportunistic tactics of nesting in excavated tunnels, which in this study is illustrated by two females which were observed taking advantage of the efforts of other females, nesting in their tunnels but without interfering with their oviposition.

Some females were observed to die whilst nesting, others were not able to oviposit after tunnel construction and were then forced to make successive attempts, and yet others only laid partial clutches, retaining some eggs in the oviduct. The inability to lay some eggs, or even the whole clutch, seems to be a cause of death in female chameleons, as only one of the 11 dead females recorded had laid a complete clutch. There is no evidence of resorption of shelled eggs in female reptiles (Blackburn, 1998), and in this study, neither a second oviposition nor expulsion of retained eggs was observed.

Mortality of female reptiles immediately after reproducing has been reported for viviparous snakes. Females in poor condition and with a high RCM commonly died, emaciated, after parturition (Madsen & Shine, 1993; Luiselli *et al.*, 1996). Similarly, we observed poor condition in chameleons, in which all but one dead female were small individuals with low body mass (excluding eggs). It is likely that, in a period of poor resource availability, these females would not be able to accumulate sufficient reserves to survive egg development, nesting and oviposition. This is also suggested by the lack of correlation between RCM and body size in dead females, whereas the correlation was significant in surviving females.

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REFERENCES

Arnall, L. & Keymer, I.F. (1975). *Bird diseases*. London: Baillère Tindall.

Blackburn, D. G. (1998). Resorption of oviductal eggs and embryos in squamate reptiles. *Herpetological Journal* **8**, 65-71.

Blasco, M., Romero, J., Sánchez, M. & Crespillo, E. (1985). La biología alimentaria y reproductora del camaleón común, *Chamaeleo chamaeleon* (L.) (Reptilia, Chamaeleonidae) de la Península Ibérica. In *El camaleón Común (Chamaeleo chamaeleon) en la Península Ibérica*, 121-148. Blasco, M., Cano, J., Crespillo, E., Escudero, J.C., Romero, J. & Sánchez, M. (Eds.). Madrid: ICONA, Ministerio de Agricultura, Pesca y Alimentación.

Bons, J. & Bons, N. (1960). Notes sur la reproduction et le développement de *Chamaeleo chamaeleon*. *Soc. Sci. Naturelles et Physiques du Maroc* **40**, 323-335.

Cuadrado, M. & Loman, J. (1999). The effects of age and size on reproductive timing in female *Chamaeleo chamaeleon*. *J. Herpetol.* **33**: 6-11.

Díaz-Paniagua, C., Cuadrado, M., Blázquez, Ma. C. & Mateo J. A. (submitted) Reproduction of *Chamaeleo chamaeleon* under different environmental conditions.

Luiselli, L., Capula, M & Shine, R. (1996). Reproductive output, costs of reproduction, and ecology of the smooth snake, *Coronella austriaca*, in the eastern Italian Alps. *Oecologia* **106**, 100-110.

Madsen, T. & Shine, R. (1993). Costs of reproduction in a population of European adders. *Oecologia* **94**, 488-495.

Schleich, H., Kästle, W. & Kabisch, K. (1996). *Amphibians and reptiles of North Africa. Biology, systematics, field guide*. Koenigsteins: Koeltz Scientific Books.

Schwarzkopf, L. (1993). Cost of reproduction in water skinks. *Ecology* **74**, 1970-1981.

Shine, R. (1980). Cost of reproduction in Reptiles. *Oecologia* **46**, 92-100.

Shine R. & Schwarzkopf, L. (1992). The evolution of reproductive effort in lizards and snakes. *Evolution* **46**, 62-75.

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