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REPRODUCTION OF CHAMAELEO CHAMAELEON UNDER CONTRASTING ENVIRONMENTAL CONDITIONS

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

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

Reproductive characteristics of *Chamaeleo chamaeleon* are described and compared between a dry and a wet year. Nesting occurred in September and October, beginning later in the dry year when females also excavated their nests in longer (but not deeper) tunnels. Females were significantly smaller, with lower body mass, lower clutch mass and lower clutch size in the dry year. Relative clutch mass and body condition did not differ between the two years. Females laid a single clutch of 4-40 eggs, with a mean relative clutch mass of 60-70%. Clutch size was correlated with maternal size, being larger in the wet year, whereas egg variables were independent of maternal characteristics. Higher mortality rate was recorded in the dry than in the wet year. The observed variation in reproductive output may be explained as a consequence of lower availability of food resources in the dry year, resulting in lower fecundity and survival of females.

Key words: chameleons, clutch size, environmental influence, maternal condition

INTRODUCTION

In reptiles, reproductive activities are influenced by environmental factors, such as temperature, rainfall and food supply. The variation in these factors are frequently associated with variation in reproductive traits, revealing their plasticity as a function of available energy (Dunham, Miles & Reznick, 1988; Seigel & Ford, 1991). Intraspecific variation in clutch size and frequency (as a consequence of different environmental causes) has been reported for several species of reptiles (Vitt, van Loben Sels & Ohmart, 1978; Seigel & Ford, 1991 and references therein), and experimental studies have demonstrated that food availability may be the main ecological factor underlying differences among individual females (Seigel & Ford, 1991; Olsson & Shine, 1997). Individual variation in reproductive output can also be explained by physical constraints, mainly related to body size, as the female abdominal cavity determines an upper limit for reproductive investment (Vitt & Congdon, 1978; Shine, 1992).

The common chameleon, *Chamaeleo chamaeleon*, inhabits a wide area around the Mediterranean sea. It is an oviparous arboreal lizard with summer courtship, autumn oviposition and a protracted incubation time (Bons & Bons, 1960; Blasco *et al.*, 1985; Cuadrado & Loman, 1999), characteristics that differentiate chameleons from the general pattern of other Mediterranean reptiles. In a previous paper, we described the process of nest construction and reported the difficulties that some female chameleons exhibit during oviposition. Females dig long and deep tunnels for nesting, and under severe drough conditions, some of them were observed to become exhausted and eventually die (Blázquez, Díaz-Paniagua & Mateo, 2000). In the present paper, we report reproductive characteristics of *Chamaeleo chamaeleon* in southern Spain and its variation in two climatically contrasting years (drought versus high rainfall). Our aim was to analyse the variation in female reproductive investment in this population, presumably as a function of environmental conditions; as it was not an experimental study, we did not pretend to establish certain correlations between reproduction and weather.

METHODS

The study was conducted in Rota and San Fernando, in Cádiz province (36° 28'N, 6° 12'W) in southern Spain, where chameleons inhabit sandy coastal areas closely associated with human activities. The study area included semi-abandoned farms and gardens, where vegetation mainly consisted of dispersed shrubs of *Retama monosperma*, and garden trees (*Myoporum tenuifolius*, *Prunus amygdalus*, *Punica granatum*, etc.). The climate is Mediterranean with hot, dry summers and mild winters, and rains fall mainly in autumn and winter.

Field work was carried out from September to November in 1995 and 1996. Climatic conditions differed remarkably between years (Fig. 1): 1995 was very dry (total rainfall November 1994-October 1995: 201mm), whereas 1996 was very wet (total rainfall November 1995-October 1996: 917 mm).

In both years we searched intensively for nesting or gravid females (which showed a voluminous clutch through the abdominal wall). Field work was concluded when no nesting females remained in the study area. Chameleons were captured by hand, and their snoutvent length (SVL) was measured to the nearest 0.5 mm. They were marked individually with spots of nail polish on the limbs (in 1995) and by claw-clipping (in 1996). Body mass was recorded to the nearest 0.5 g with a spring dynamometer before oviposition (BMB) and after oviposition (BMA), whenever possible. When both

Correspondence: Carmen Díaz-Paniagua, Estación Biológica de Doñana, Apartado 1056, 41080 Sevilla, Spain. *E-mail*: paniagua@cica.es

TEMPERATURE (C) 40 30 20 10 S N S N Μ S N J Μ Μ J J Μ J 1994 1995 1996

FIG. 1. Monthly variation in rainfall (bars) and mean temperature (broken line) during the period of study of reproduction by chameleons in southern Spain. Horizontal bars above the histogram indicate the nesting season in each study year.

values were recorded for an individual female, their difference (BMB-BMA) was considered as an approximation of the clutch mass (ACM). This measure is not an entirely satisfactory measure of clutch mass, but we considered it appropriate to describe the high increment in mass supported by females due to their reproductive investment. BMB was the maximum body mass of egg-bearing females, recorded on dates close to oviposition, whereas BMA was recorded from 0 to 2 days after nesting. Relative clutch mass (RCM) was estimated as the ratio ACM/BMA (following Shine, 1980).

Clutch size (CS) was recorded either by opening the nests immediately after egg-laying (n=19 in 1995), after eggs had hatched (n=5 in 1995, n=24 in 1996), and from dissection of gravid females found dead (five in 1995 and one in 1996). Egg length (EL), egg width (EW) and egg mass (EM) were recorded on the nesting day for 19 clutches in 1995. In 1996 we measured only four eggs in each of 35 clutches. Egg shape was calculated as the ratio of EL to EW.

Nests were located when we observed females excavating on the ground, and by tracks left on the sand by females after nesting. The depth (vertical distance from the ground surface to the egg chamber) and length of the nest tunnel were measured in 14 nests in 1995 and 23 in 1996.

Mean values per clutch were used in all statistical analyses. Variables were compared among females and between the two study years using ANOVA and Pearson correlation. Correlations between length variables (SVL, EL, EW) and mass variables (BMA, BMB, ACM, EM) were made after their logarithmic transformation. The physical condition of females after nesting was analysed by using the residual scores from the regression of log BMA to log SVL for the pooled data of 1995 and 1996 (see e.g. Madsen & Shine, 1999). Differences in CS between years were analysed by comparing the regression lines of CS on female SVL. An ANCOVA was used to analyse the variation in RCM in the two study years, in which ACM was the dependent variable, BMA was the covariate, and year was the class variable.

RESULTS

400

300

REPRODUCTIVE PHENOLOGY AND NEST CHARACTERSTICS

In 1995 we found 65 nests, and the nesting season extended from 25 September to 7 November, with a peak in mid October. In 1996 we found 53 nests and the nesting season extended from 19 September to 28 October, with a peak in the first week of October (Fig. 2). Mean egg-laying date differed significantly between years ($F_{1,116}$ =26.21, P<0.0001), with females nesting earlier in the wet year.

Mean tunnel length was 52 cm (SD=16.7, range: 23-87, n=14) in 1995 and 39 cm (SD=15.17, range: 20-80, n=53) in 1996, and differed significantly between years $(F_{1,36} = 6.51, P=0.015)$. Nest depth averaged 32 cm (SD=7.4, range: 18-42) and 36 cm (SD=9.3, range: 15-60), respectively, but did not differ statistically between years (P>0.05).



FIG. 2. Frequency distribution of the number of nests found each week during the period of study of reproduction by chameleons in southern Spain.

	SVL (mm)	BMB (g)	BMA (g)	ACM (g)	RCM (%)	CS No. eggs
1995						
Mean	96.6	31.1	24.1	13.0	60.5	11.2
SD	11.2	8.6	7.2	6.5	29.8	4.4
Range	75-130	18-56	11.3-50.0	2-26	10.5-102.9	4-21
n	84	53	34	19	17	29
1996						
Mean	117.0	51.1	30.8	21.0	70.2	17.9
SD	11.1	13.3	59.8	7.1	17.7	6.4
Range	97-144	31.1-8.8	19.6-50.6	11.1-39.1	42.5-111.2	7-40
n	50	43	53	36	36	25
F	104.32	79.37	20.26	12.77	1.00	19.78
Р	< 0.005	< 0.005	< 0.005	< 0.005	0.321	< 0.0005
df	1,132	1,94	1,101	1,54	1,36	1,53

TABLE 1. Reproductive characteristics of female chameleons in 1995 and 1996, and the results of ANOVA comparing data from 1995 and 1996. (SVL: snout-vent length, BMB: body mass before oviposition, BMA: body mass after oviposition, ACM: approximated clutch mass = BMA-BMB, RCM: relative clutch mass= ACM/BMA, CS: clutch size).

CHARACTERISTICS OF GRAVID FEMALES

Mean body size of reproductive females was smaller in the dry year than in the wet year (Table 1). The smallest gravid female in 1995 was 75 mm SVL (with BMA as low as 11.3 g) and 97 mm in 1996. The approximate clutch mass was smaller in the dry than in the wet year (Table 1), in accordance with the smaller body size of females. The clutch mass was correlated significantly with SVL (after logarithmic transformation of the two variables r=0.731, P<0.0001) and with BMA (r=0.625, P<0.0001) for data pooled over two years. For each



FIG. 3. Relationship between snout-vent length and clutch size of female chameleons in 1995 (filled circles) and 1996 (squares) in southern Spain.

year, only the relationship between ACM and BMA in 1995 was not significant.

Female chameleons averaged a clutch mass relative to their body mass of 60.5% and 70.2% in 1995 and 1996, respectively. Some individuals in each year had a clutch mass as high as their own body mass (RCM»100%). Although females in 1995 were smaller and had a wider range of RCM than in 1996, we did not find a significant difference in mean RCM (Table 1). The ANCOVA with ACM as the dependent variable and BMA as covariate revealed a similar relationship between body mass and clutch mass in the two years (slopes: $F_{1,44}$ =0.539, P=0.467; intercepts: $F_{1,44}$ = 0.144, P=0.706).

Clutch size ranged from 4 to 21 eggs in 1995 and from 7 to 40 eggs in 1996, and differed significantly between years (Table 1). Clutch size and SVL were correlated significantly in both years (1995: r=0.659, P=0.0005; 1996: r=0.825, P<0.0005). The slopes of the regression lines in 1995 and 1996 were not homogeneous (slopes: $F_{1,42}=17.800$, P=0.0001), indicating that CS increased more with SVL in the wet than in the dry year (Fig. 3).

The logarithmic regression of SVL and BMA was significant for pooled data from both study years $(R^2=0.509)$, and residual scores did not reveal significant differences in body condition of females between 1995 and 1996. Within each year, the regression was also significant, with $R^2=0.263$ in 1995 and $R^2=0.645$ in 1996, and they differed significantly in their slopes (Fig. 4; slopes: $F_{1,91}=5.297$, P=0.024), suggesting that the lower BMA in the dry year was more related to the smaller body size of females than to environmental differences between years.



FIG. 4. Relationship between the logarithm of snout-vent length and body mass of female chameleons after oviposition, indicative of their physical condition (filled circles: 1995; squares: 1996).

MORTALITY OF NESTING FEMALES

Out of a total of 84 gravid females monitored in 1995, 14 were found dead: one was killed by a cat, two were run over by vehicles and 11 did not show external damage. We assumed the latter had died as a consequence of stress related to reproduction (see Blázquez *et al.*, 2000). In 1996, two out of 50 gravid females were found dead during the nesting season: one was run over, and the other was eaten by a snake while excavating the tunnel nest; no other dead females were found. The observed mortality was significantly different between years (χ^2 =4.78, *P*=0.029).

EGG CHARACTERISTICS

Egg variables did not differ between years but varied significantly among clutches (Table 2). Egg mass was positively related with EL (r=0.610, P=0.0001) and EW (r=0.708, P<0.0001), but not with egg shape. No correlation was observed between any of the egg variables with CS, SVL or BMA, but EW and egg shape were significantly related to RCM (EW: r=0.479, P=0.02; shape: r=-0.445, P=0.033).

DISCUSSION

Reproductive investment by female chameleons is relatively high. A single clutch is produced per year, which may reach 100% RCM in some individuals. Mean RCM obtained in this study ranks among the highest in reptiles, comparable to the RCM of viviparous terrestrial snakes (see Shine, 1992 for a review). Large clutch volumes and high RCM have mostly been described for reptiles with cryptic behaviour that use sit-and-wait foraging, for which the probability of escaping predators does not depend on rapid movements (Vitt & Congdon, 1978; Vitt & Price, 1982; Dunham et al., 1988). Chamaeleo chamaeleon is a good example of a species for which a high RCM should not greatly influence either the probability of escaping predators or foraging efficiency, although the high volume of the clutch may decrease the ingestion rate of females during the late gravid period (Bons & Bons, 1960).

Environmental conditions apparently influenced the timing of reproduction; the nesting season of chameleons started later in the dry year than in the wet year. One explanation may be that females delayed oviposition in the dry year while waiting for better environmental conditions, and thus retained eggs in the oviduct for longer in 1995 than in 1996 (see Bons & Bons, 1960). The

TABLE 2. Descriptive statistics of chameleon egg length (EL, in mm), width (EW, in mm), mass (EM, in g), and shape (EL/EW) in 1995 and 1996, and results of ANOVA within and between years. Values were averaged per clutch, except for the range, which is given over the total egg number. n = number of clutches. ***P<0.0005; NS P>0.05.

	EL	EW	EM	Shape
1995				
Mean	16.82	10.49	1.16	1.60
SD	1.15	0.46	0.16	0.14
Range	13.7-21.3	8.6-11.7	0.8-1.5	1.4-2.0
n	19	19	19	19
$F_{18,199}(1995)$	57.89***	22.52***	33.91***	
1996				
Mean	16.44	10.76	1.204	1.53
SD	0.91	0.53	0.20	0.09
Range	10.6-19.6	7.6-12.1	0.7-1.8	1.4-1.7
n	35	35	35	35
$F_{_{34,188}}(1996)$	7.59***	23.18***	43.23**	
$F_{1,48}(1995 \times 1996)$	1.2 ^{NS}	2.91 ^{NS}	0.73 ^{NS}	

1995 delay in the nesting season may also be related to the smaller size of females in that year. Cuadrado & Loman (1999) found that female size was correlated with reproductive timing, presumably because of a later attainment of sexual maturation in young (small) females, or because small females secure more resources for reproduction by extending the time that resources are allocated to follicles.

Nesting in chameleons often starts after the first autumn rains (Bons & Bons, 1960; Schleich, Kästle & Kabish, 1996), which probably favours nesting conditions and facilitates tunnel excavation in more compacted sandy soils. In our study, the nests were located deep in the substrate, which may insure adequate moisture conditions during the long incubation period. Difficulty in finding optimal nest conditions may be the reason for the excavation of longer tunnels in the dry year, although their depth was similar in the two years. Blasco *et al.* (1985) reported shorter tunnel length and lower nest depth for other localities from south-eastern Spain, which suggests that nest characteristics may vary among populations as a function of environmental conditions and soil characteristics

Dunham (1983) demonstrated a correlation between the amount of rainfall and the availability of food resources to insectivorous lizards. Accordingly, we assumed that the drought conditions in 1995 reduced the availability of food resources in the study area. In 1995 reproductive females reached smaller body size than in 1996. Consequently, the interannual variation observed in CS and ACM is mainly explained by the variation in female body size, as fecundity is normally associated with this (see e.g. Roff, 1992).

In contrast, relative clutch mass did not differ significantly between years, and females made a similar investment in reproduction, independently of their body mass. In other species, the variation in RCM has been associated with different climatic conditions and resource availability (Vitt & Price, 1982). However, RCM remained remarkably constant for individuals of Lacerta agilis reared under both high and low resource availability (Olsson & Shine, 1997). A similar situation occurred in chameleons, for which the same investment is made by females in years of low and high availability of resources. However, the wide variation in RCM among chameleons suggests different responses by individual females, especially in the year of lower resource availability, which is supported by the lack of correlation in 1995 of ACM with BMA.

Egg characteristics (length, width and mass) remained constant despite the between-year variation observed in clutch size and female body size and mass. Egg variables were also similar to those described for other Spanish populations (Blasco *et al.*, 1985), which supports the idea of an optimal egg size (*sensu* Smith & Fretwell, 1974; Brockelman, 1975) for this species. According to optimal egg size theory, egg dimensions are limited by the minimum size that enables hatchling survival; the theory predicts that clutch size, rather than egg and offspring size, varies with fluctuating resource availability (Brockelman, 1975). In our study the larger body size of female chameleons resulted in an increase in the number rather than size of eggs. Shape and width were the only egg variables related with RCM. Eggs were less elliptical in larger clutches, which could result from the effect of egg packaging inside the abdominal cavity.

The high mortality of reproducing females in 1995 can be explained either by a higher than optimal investment in reproduction by particular females, as suggested by the wide variation in RCM, or by their small body size which probably caused difficulties during egg-laying and even caused egg retention after oviposition (Blázquez *et al.*, 2000). These difficulties can be associated with the fact that a similar egg size is borne by small and big females.

Our results indicate that female reproductive investment by chameleons does not vary with environmental conditions, but under poor conditions females are smaller and consequently have lower clutch sizes than in years of high food resources. Chameleons produce a single clutch per year and their reproductive output is therefore constrained by the female abdominal cavity and physiological limitations. Under an overall perspective, the reproductive output of a chameleon population may be considered to vary according to environmental conditions, as lower fecundity and higher mortality of nesting females in dryer years than wet years results in lower juvenile recruitment.

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