# The Effects of Age and Size on Reproductive Timing in Female Chamaeleo chamaeleon

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ABSTRACT.—Reproductive timing in relation to the size and age of individual female common Chameleons (*Chamaeleo chamaeleon*) was studied in a population in southern Spain. Thirty-one radio-tagged females were observed during two summers, 1993 and 1995. The mating season (courting, pair formation, and copulation) lasted from late July to mid-September. Egg-laying was recorded from 25 September to 28 October, 34–40 d after copulation. Timing of reproduction varied between individual females, old and large females timing the reproductive events (i.e., mating and egg-laying) earlier than young and small ones. Specifically, timing was affected by size when age was controlled for but not the reverse. Four alternative explanations for delayed breeding of younger and smaller female chameleons are discussed: (1) late breeding could be a consequence of physiological constrains in the onset of maturation of younger females; (2) late breeding allows young females to secure more resources for reproduction thus achieving larger clutches; (3) young females avoid competition for attractive males from large females, and (4) if young females are less preferred, they may not be courted until males no longer are courting larger females. This happens when the latter become pregnant.

RESUMEN.—En este trabajo se analiza el efecto del tamaño y la edad de la hembras en la fenología reproductiva de una población de Camaleón Común del sur de España. Para ello se estudió el ciclo reproductor de 31 hembras mediante radio-emisores durante dos veranos (1993 y 1995). Cada año, la estación reproductora (cortejo, emparejamiento y cópula) comenzó a finales de Julio y terminó a mediados de Septiembre. La puesta tuvo lugar desde el 25 Septiembre al 28 Octubre, entre 34 y 40 días después de la cópula. La fenología reproductora estuvo relacionada con el tamaño (no la edad) y así, las hembras de mayor tamaño comenzaron y completaron la reproducción significativamente antes que las hembras de menor tamaño: (1) la adquisición de la madurez sexual en las hembras jóvenes retrasa su reproducción; (2) el retraso en la reproducción y posiblemente, una mayor fecundidad; (3) la reproducción tardía evitaría la competencia intrasexual con las hembras de mayor tamaño por los machos más atractivos y (4) los machos prefieren a las hembras de mayor tamaño y por tanto, se reproducen con las más pequeñas una vez que aquellas están grávidas.

Many aspects of reproductive behavior are known to be influenced by age and size of the female (Searcy, 1982; Bateson, 1983; Andersson, 1994). There are numerous examples where age at sexual maturity differs among individuals of the population (e.g., Immelmann, 1971; Aleksiuk and Gregory, 1974; Kevles, 1986; McLain et al., 1993). Also, the timing of reproductive events within a reproductive cycle may vary among individuals, with older females completing their reproduction earlier than younger ones (Bauwens and Verheyen, 1985; Noltie and Keenleyside, 1987; Ridgway et al., 1991; Danylchuk and Fox, 1996). Furthermore, reproductive success is often age dependent, especially in species with continuous growth (e.g., Fitch, 1975; Madsen et al., 1993). Therefore, female size influences the pattern of sexual selection among individuals. In many species, large females are preferred by males as mates (Ferguson and Fox, 1984; Bauwens and Verheyen, 1985, 1987; Verrell, 1985, 1994; Gibbons and MacCarthy, 1986; Holmberg, 1991; Olsson, 1993; Danylchuk and Fox, 1996), because size is often positively correlated with either female reproductive success (e.g., Olsson, 1993; see Dunham and Miles, 1992; Roff, 1993 for reviews) or offspring survival (Ferguson and Fox, 1984; Ford and Seigel, 1989). In consequence, both variables are known to have important evolutionary consequences for the dynamics of the population.

The common chameleon, *Chamaeleo chamaeleon*, is an insectivorous, medium-sized lizard found in North Africa, southern Europe, and the Middle East. It is a single-clutched oviparous species (Romero, 1984; Fernández, 1985, 1989; Blasco et al., 1985) with an early maturation (i.e., eggs hatch in late summer and autumn and both sexes reach sexual maturation in their first

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summer the following year; see also Fernández, 1988). Eggs are laid in autumn and the eggs hatch after 9-12 months (Blasco et al., 1985; González, 1989). Female chameleons, like many other species, are receptive to mating during a short period each year (e.g., Immelmann, 1971; Kevles, 1986; McLain et al., 1993) and, as in many other reptiles, males are rejected by females outside the receptive period (e.g., Edsman, 1990; Fry, 1991; Olsson, 1993). Their reproductive behavior can be monitored closely and female age and size varies substantially within a population. In this study, we describe the timing of reproduction and analyze the separate effects of age and size on reproductive behavior. To our knowledge, this is the first time these aspects have been reported for a chameleon.

## MATERIAL AND METHODS

Study Site.-Chameleons were studied at the gardens of the Real Instituto y Observatorio de la Armada, an astronomical observatory of the Spanish Navy located in centre of San Fernando (Cádiz, S Spain, 36°28'N, 6°12'W). This is at the northern limit of the species' distribution, at the southwest coast of Spain (Blasco et al., 1985; Cuadrado and Rodríguez, 1997). The Observatory is surrounded by unsuitable habitats for the species (built-up areas and roads). The vegetation is characterized by tall trees (Cupressus sempervirens, Myoporus tenuifolium, Salix spp., and Eucalyptus spp.), several shrubland bushes (Retama monosperma, Nerium oleander, and Rosmarinum officinalis) and climbing plants (e.g., Hedera *helix*). Some bare ground areas are also present.

*Field Observations.*—The population was visited every day during the period 20 July to 6 October in 1993 and 25 May to 25 November in 1995. These periods cover courting, pair formation, and copulations of all females.

The behavior of 31 females was monitored closely (16 in 1993 and 15 in 1995). This includes five females born in the previous autumn and 26 older individuals. To facilitate the continuous monitoring of these females they were equipped with radio transmitters. We used BD-2G transmitters (1.85 g, 151 kHz, Holohil Systems Ltd.) and a TELEVILT receiver (RX-8910) to follow the activities of radio-tagged females. Transmitters represented ca. 3–14% of female body mass. They were built in an inverted V-shape to securely fit on the females' back, and glued (Loctite®) to the skin. After the receptivity period, all females in the population, including those without transmitters, were checked for signs of pregnancy (non-receptive color or round swollen body shape) and measured.

All chameleons found since 1992 were captured and individually marked by cutting a unique combination of claws for individual recognition. One claw per foot, involving at most three feet, were clipped. Most chameleons were marked as juveniles, i.e., during their first calendar year. Most captures were made at night when chameleons are easily detected with a strong head lamp. Chameleons were captured by hand, marked, and released after recording identity, sex, age, and snout-to-vent length (SVL). All chameleons were released within 1 h at their place of capture. In autumn and beginning of their first summer the youngest cohort could easily be distinguished from older chameleons by their smaller size and other features such as the presence of black color inside their mouth, which is totally absent in older individuals (M. Cuadrado, pers. obs.). We separated two age classes: chameleons in their second calender year (i.e., born in a previous year) were classified as young (i.e., one year old) and separated from older lizards on the basis of size at first capture.

Behavioral Observations.-The following variables were defined to characterize the timing of reproduction for each female: (1) The first day a female was courted. Males' courting behavior included active display (i.e., sidewise exhibition of a laterally flattened body and a tightly curled tail), specific body color patterns (dark green body background with cloudy black spots), and the male following and guarding the female at a close distance throughout her home range (Cuadrado, 1998a). This may or may not take place before the formation of a pair. (2) The first day in pair. A pair is here defined as a male and a female observed together (i.e., <4 m from each other) for at least two consecutive days; (3) The first observation of 'receptive' body colors (Cuadrado, 1998b). From a given day onwards, females exhibit conspicuous and easily distinguishable body color patterns. These patterns include a leaf green background color, sometimes brown, with conspicuous yellow or sometimes orange or green, spots. Most copulations occur when females exhibit this color pattern (Cuadrado, 1998b) and hence, we define it as the receptive color. In total, 26 out of 31 females showed receptive colors, including all that were observed copulating. (4) Date of copulation. Some females copulated several times, with one or more males (Cuadrado and Loman, 1997; Cuadrado, in press). (5) First day with non-receptive colors. Shortly after copulations females change to another color pattern. The background color changes from green or brown to black, but the yellow, orange, green and sometimes bluish spots remain (Valverde, 1982; Romero, 1984; Blasco et al., 1985). (6) Date of egglaying. Females dig a burrow and deposit the eggs. All females laying eggs were recorded not only those with transmitters. This was done in

TABLE 1. Results of five different ANCOVA's testing the independent effects of year, size and age of the female on aspects of the reproductive timing of female chameleons with size as covariate. All interactions were found non-significant and removed from the final analysis.

Dependent variable	Effect	df	F	Р
First day of courting	Size Age Year	1:26 1:26 1:26	6.01 0.00 0.23	0.020 0.981 0.630
First day in pair	Size Age Year	1:23 1:23 1:23	9.30 0.04 0.23	0.006 0.827 0.630
First day with receptive colors	Size Age Year	1:21 1:21 1:21	5.68 7.54 7.38	0.027 0.228 0.013
Day of (first) copu- lation	Size Age Year	1:12 1:12 1:12	11.52 2.12 2.61	0.005 0.163 0.132
First day with non- receptive colors	Size Age Year	1:18 1:18 1:18	46.05 4.05 4.76	0.000 0.059 0.042

1995. Date for egg-laying of 21 females was recorded.

#### RESULTS

Timing of Reproductive Behavior.-Each year the mating season started with male courting, male display, and pair formation. All radio-tagged females were visited (i.e., a male was closer than 4 m) and courted (see methods) by at least one male. However, only 28 paired with a male. Overall average dates of first courting and first pairing were 17 August (range: 28 July-10 September, N = 31) and 20 August (range: 28 July-8 September, N = 28), respectively. There was no significant difference in date of first courting (ANOVA,  $F_{1,29} = 1.8$ , P = 0.18) and pairing (AN-OVA,  $F_{1,26} = 0.1$ , P = 0.72) between years (Table 1). Females shifted to receptive body colors before copulations. Mean dates of first observation of this pattern were 1 September in 1993 (range: 26 August-11 September, N = 11) and 26 August in 1995 (range = 17 August-13 September, N = 15). This date differed significantly between years (ANOVA,  $F_{1,24} = 4.5$ , P = 0.04; Table 1). Mean date of copulations were 2 September (range: 22 August–13 September). There was no significant difference between years (ANOVA,  $F_{1.15} = 0.0$ , P = 0.82; Table 1). Mean date for the first observation of non-receptive colors was 3 September (range: 25 August–13 September). There was no significant difference between years ( $F_{1.21} = 0.0$ , P = 0.98). However, we obtained a significant effect of year when age and size were controlled for (Table 1). Later in the season females dog a hole for oviposition. The average time for egg-laying in 1995 was 9 October (range = 25 September to 28 October). The time between copulation and egg-laying was measured for four females, all older than 1 year. These times were 34, 34, 37, and 40 d.

Breeding of Young Females.—All females more than one year old were breeding, i.e., they were seen copulating and/or carried the typical color of pregnant females. However, a large fraction 1993: 11 of 24 (46%), 1995: 11 of 26 (42%) of young females were non-reproductive. Those young females that were breeding were significantly larger than those that were not (Table 2).

Age and Size-Related Differences.—There was considerable variation among individual females in the timing of reproductive events. In general, older females timed their behavior earlier than younger ones. Courting, pairing, first exhibition of receptive colors, copulations, and egg-laying occurred about one week earlier for older females (Table 3). However, older females were also significantly larger than the younger ones (Table 4). In order to separate the effects of these factors for reproductive timing, we performed an ANCOVA with date as a dependent variable, year, age, and size as independent variables and size as covariate. After correcting for the effect of age, female size had a significant effect on the timing of all reproductive events (Table 1). However, there was no independent effect of age on any of the variables (Table 1).

### DISCUSSION

Our results show that timing of reproduction varied among females and that both age and size are correlated with the individuals' timing. Both factors are known to influence the reproductive activities for many taxa including fishes (Noltie and Keenleyside, 1987; Ridgway et al., 1991; Danylchuk and Fox, 1996), reptiles (e.g.,

TABLE 2. Size (SVL, mm) of pregnant and non-pregnant female chameleons of the youngest cohort (ageclass 1, see methods). Figures represent mean values  $\pm$ SE. Sample sizes in parentheses.

Year	Nonpregnant	Pregnant	Test for differences
1993 1995	$82.6 \pm 2.3 (N = 11) \\ 87.5 \pm 1.7 (N = 11)$	$95.6 \pm 2.1 (N = 13)$ $102.4 \pm 1.4 (N = 15)$	t = 4.125, P < 0.001 t = 5.709, P < 0.001
Total	$85.0 \pm 1.5 (N = 22)$	$99.2 \pm 1.3 (N = 28)$	t = 7.260, P < 0.001

TABLE 3. Timing of reproductive events for female chameleons of different age groups. Dates represent mean values ±standard error of mean. Sample sizes are given in parentheses. Females included were monitored with radio transmitters, except for data on egg laying. For that, information on all females observed laying eggs are included. (a) Not recorded.

	Year	1	>1
First day of courting	1993	Aug. $30 \pm 1.05$ (2)	Aug. $19 \pm 3.1 (14)$
	1995	Aug. $21 \pm 5.3$ (3)	Aug. $13 \pm 3.3 (12)$
First day in pair	1993	Sept. $4 \pm 5.5$ (2)	Aug. $18 \pm 3.4$ (12)
	1995	Aug. $30 \pm 5.8$ (3)	Aug. $16 \pm 3.7$ (11)
First day with receptive colors	1993	(a)	Sept. 1 $\pm$ 1.5 (11)
	1995	Sept. 5 ± 5.4 (3)	Aug. 24 $\pm$ 2.0 (12)
Day of (first) copulation	1993	(a)	Sept. $1 \pm 2.3$ (9)
	1995	Sept. 4 ± 4.9 (3)	Sept. $1 \pm 4.2$ (5)
First day with non-receptive colors	1993	Sept. 12 (1)	Sept. $2 \pm 1.7$ (11)
	1995	Sept. 5 ± 6.5 (2)	Sept. $3 \pm 2.7$ (9)
Day of egg-laying	1995	Oct. $19 \pm 2.8 (5)$	Oct. 10 ± 1.8 (16)

Bauwens and Verheyen, 1985; Olsson, 1993; Galán, 1995; Olsson and Shine, 1996), and birds (e.g., Loman, 1984; Enoksson, 1993). In chameleons, old (large) females started and completed their reproductive activities earlier than young (small) ones. The detailed analysis however, showed that the key factor probably is size, not age. Also, size influences age of first reproduction in this chameleon. This is similar to what has been found for other reptiles (Madsen and Shine, 1992) and underlines the importance of size for reproductive strategies (see also Olsson and Shine, 1997).

Age and size are also known to influence other aspects of the reproduction in this chameleon. For instance, larger (older) females are preferred by males as sexual partners; they attracted more males and are courted and guarded for longer periods (Cuadrado and Loman, 1997; Cuadrado, 1998a; see also Fitzgerald, 1982; Olsson, 1993 for a similar pattern in other reptiles).

Basically, we see four alternative explanations for this age- and size-related reproductive timing: (1) Early breeding might give benefits to females and hence, all females irrespective of their age (size) try to breed as soon as possible. These benefits could be a head start for the off-

TABLE 4. Size (SVL, mm) of female chameleons from different age classes. Values represent mean  $\pm$ standard error of mean. Sample sizes are given in parentheses.

	Age class		
	1	>1	
1993 1995 Both years	$\begin{array}{c} 85.7 \pm 2.0 \ (4) \\ 105.3 \pm 5.1 \ (3) \\ 94.1 \pm 3.2 \ (7) \end{array}$	$\begin{array}{c} 109.0 \pm 1.1 \ (14) \\ 114.5 \pm 3.1 \ (12) \\ 111.5 \pm 1.6 \ (26) \end{array}$	

spring, with higher rates of survival, and a longer feeding period for the female before hibernation (see Olsson and Shine, 1997 and references therein). Late reproduction, including first mating of juvenile females, could therefore be a consequence of a physiological constraint in the onset of sexual maturation, as observed in other reptiles (Bauwens and Verheyen, 1985; Olsson, 1993; Galán, 1995). Actually, our data suggest a threshold size of about 90 mm for young females to successfully achieve and complete reproduction in the first year (Table 2; see also Fernández, 1988). In a recent study, Olsson and Shine (1997) reported strong evidence of the physiological constraints hypothesis. In a field study of sand lizards (Lacerta agilis), early egglaying females were "large individuals in good physical condition that had grown rapidly in previous years" (Olsson and Shine, 1997). (2) Late breeding of young (small) females is adaptive. Assume, for instance, that late breeding allows a female to secure more resources and hence have a larger clutch than would be possible with early breeding. This is probably true for all females and is balanced by the disadvantages of a late clutch (see above). However, under this scenario the optimum timing for breeding will be later for young females if they grow more rapidly than for the larger, more slowgrowing, ones. (3) If males prefer large (more fecund) females as potential mates, small females may avoid competition for attractive males from large females by delaying their receptivity (see references above). A delayed breeding could therefore also favor multiple mating, which, in turn, may enhance the survival of offspring (Olsson and Shine, 1997). (4) If males prefer large females, small females may simply have to passively wait, receptive or not, until large females become pregnant and the males direct their attention to smaller ones.

Whatever the cause, the female breeding asynchrony observed in our study increases male variance in reproductive success. Breeding asynchrony allowed competitively superior large male chameleons to increase their reproductive success by first mating with large females and later with smaller ones (Cuadrado and Loman, 1997; Cuadrado, *in press*; see also Johnstone, 1997).

Characteristics of this chameleon population seem to fulfil the basic assumptions of all these four alternatives and only carefully planned experiments can separate them. The aim of our study was to provide a descriptive basis for such work. However, one observation in support of the second hypothesis is worth noting. The mechanism suggested only operates in a species with summer/autumn breeding that includes both courtship, copulation, and production of offspring. In these species, females use resources secured during the breeding period to produce the clutch. In spring breeding species, in contrast, the clutch is produced from resources secured during the previous season, so young females have no direct advantage from delaying breeding. The former breeding pattern is not common, the Common Chameleon being one of the few. Thus, if the second explanation is true, it may be no surprise that few studies have observed the difference in reproductive timing between large and small females that were recorded in this study.

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## LITERATURE CITED

- ALEKSIUK, M., AND P. GREGORY. 1974. Regulation of seasonal mating behaviour in *Thamnophis sirtalis* parietalis. Copeia 1974:681–689.
- ANDERSSON, M. 1994. Sexual Selection. Princeton Univ. Press, Princeton, New Jersey.
- BATESON, P. (ed.). 1983. Mate Choice. Cambridge Univ. Press, Cambridge.
- BAUWENS, D., AND R. F. VERHEYEN. 1985. The timing of reproduction in the lacerta lizard Lacerta vivi-

para: differences between individual females. J. Herpetol. 19:353–364.

- , AND ——. 1987. Variation of reproductive traits in a population of the lizard *Lacerta vivipara*. Holartic Ecology 10:120–127.
- BLASCO, M., J. CANO, E. CRESPILLO, J. C. ESCUDERO, J. ROMERO, AND J. M. SANCHEZ. 1985. El Camaleón Común (*Chamaeleo chamaeleon*) en la Península Ibérica. ICONA, Ministerio Agricultura Pesca y Alimentación, Madrid.
- CUADRADO, M. 1998a. The influence of female size on the extent and intensity of mate guarding by males in *Chamaeleo chamaeleon*. J. Zool. (London) 246:351– 358.
- —, 1998b. The use of yellow spot colors as a sexual receptivity signal in female Chamaeleo chamaeleon. Herpetologica 54:395–402.
- in press. Mating asynchrony favours no assortative mating by size and serial-type polygyny in common chameleons, *Chamaeleo chamaeleon*. Herpetologica.
- —, AND J. LOMAN. 1997. Mating behaviour in a chameleon (*Chamaeleo chamaeleon*) population in southern Spain—effects of male and female size. *In* W. Böhme, W. Bischoff, and T. Ziegler (eds.), Herpetologica Bonnensis. pp. 81–88. Bonn.
- ——, AND M. RODRIGUEZ. 1997. Distribución actual del camaleón en la península Ibérica. Quercus 133: 31–36.
- DANYLCHUK, A. J., AND M. G. FOX. 1996. Size- and age-related variation in the seasonal timing of nesting activity, nest characteristics and female choice of parental male pumpkinseed sunfish (*Lepomis gibbosus*). Can. J. Zool. 74:1834–1840.
- DUNHAM, A. E., AND D. B. MILES. 1992. Patterns of covariation in life history traits of squamate reptiles. The effects of size and phylogeny reconsidered. Amer. Natur. 126:231–257.
- EDSMAN, L. 1990. Territoriality and competition in wall lizards. Unpubl. Ph.D. Thesis, Stockholm Univ., Stockholm.
- ENOKSSON, B. 1993. Effects of female age on reproductive success in European nutnatches breeding in natural cavities. Auk 110:215–221.
- FERGUSON, G. W., AND S. F. FOX. 1984. Annual variation in survival advantage of large hatching sideblotched lizards, *Uta stansburiana*: its causes and evolutionary significance. Evolution 28:342–349.
- FERNANDEZ, F. 1985. Biología y comportamiento del camaleón común Chamaeleo chamaeleon. Unpubl. M.S. Thesis, Sevilla Univ., Sevilla.
- ------. 1988. La adquisición de la madurez sexual en el camaleón común (*Chamaeleo chamaeleon*). Doñana, Acta Vertebrata 15:225–227.
- ——. 1989. Comportamiento reproductor del camaleón común (*Chamaeleo chamaeleon L.*) en el sur de España. Doñana, Acta Vertebrata 16:5–13.
- FITZGERALD, K. T. 1982. Mate selection as a function of body size and male choice in several lizard species. Unpubl. Ph.D. Diss., Univ. Colorado, Boulder.
- FITCH, H. 1975. A demographic study of the ringneck snake (*Diadophis punctatus*) in Kansas. Univ. Kansas. Mus. Natural History Misc. Publ. No. 62:1–53.
- FORD, N. B., AND R. A. SEIGEL. 1989. Relationships among body size, clutch size and egg size in three

species of oviparous snakes. Herpetologica 45:75-84.

- FRY, F. L. 1991. Reptile Care. An Atlas of Diseases and Treatments, Vol. II. T.F.H. Public, Inc., New Jersey.
- GALAN, P. 1995. Ecología reproductora de la lagartija de Bocage. Quercus 117:35–39.
- GIBBONS, M. M., AND T. K. MACCARTHY. 1986. The reproductive output of frogs *Rana temporaria* (L.) with particular reference to body size and age. J. Zool. (London) 209:579–593.
- GONZALEZ, J. P. 1989. Anfibios y reptiles de la provincia de Huelva, 2nd ed. Imprenta Jiménez, Huelva.
- HOLMBERG, K. 1991. Mallard ducks, mate choice and breeding success. Ph.D. Thesis, Stockholm Univ., Stockholm.
- IMMELMANN, K. 1971. Ecological aspects of periodic reproduction. In D. S. Farner, J. R. King, and K. C. Parkes (eds.), Avian Biology, Vol. 1, pp. 341–389. Academic Press, New York. JOHNSTONE, R. A. 1997. The tactics of mutual mate
- JOHNSTONE, R. A. 1997. The tactics of mutual mate choice and competitive search. Behav. Ecol. Sociobiol. 40:51–59.
- KEVLES, B. 1986. Females of the Species. Sex and Survival in the Animal Kingdom. Harvard Univ. Press, Cambridge.
- LOMAN, J. 1984. Breeding success in relation to parent size and experience in a population of Hooded Crow. Ornis Scand. 15:183–187.
- MADSEN, T., AND R. SHINE. 1992. Cost of reproduction in female adders, *Vipera berus*. Oecologia 92:40–47.
- MADSEN, T., R. SHINE, J. LOMAN, AND T. HAKANSSON. 1993. Determinants of mating success in male adders, *Vipera berus*. Anim. Behav. 45:491–499.
- MCLAIN, D. K., L. B. BURNETTE, AND D. A. DEEDS. 1993. Within season variation in the intensity of sexual selection on body size in the bug *Margus obscurator* (Hemiptera Coreidae). Ethology Ecology Evolution 5:75–86.

- NOLTIE, D. B., AND M. H. A. KEENLEYSIDE. 1987. Breeding ecology, nest characteristics, and nest-site selection of stream- and lake-dwelling rock bass, *Ambloplites rupestris* (Rafinesque). Can. J. Zool. 65: 379–390.
- OLSSON, M. 1993. Male preference for large females and assortative mating for body size in the sand lizard (*Lacerta agilis*). Behav. Ecol. Sociobiol. 32:337– 341.
- —, AND R. SHINE. 1996. Does reproductive success increase with age or with size in species with indeterminate growth? A case study using sand lizards (*Lacerta agilis*). Oecologia 105:175–178.
- ——, AND ——, 1997. The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. J. Evol. Biol. 10:369–381.
- RIDGWAY, M. S., B. J. SHUTER, AND E. E. POST. 1991. The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass, *Micropterus dolomieui* (Pisces: Centrarchidae). J. Anim. Ecol. 60:665–681.
- ROFF, D. A. 1993. The Evolution of Life Histories. Chapman and Hall Inc., New York.
- ROMERO, J. 1984. Contribución al conocimiento de la morfología y biología de Chamaeleo chamaeleon (L.). Unpubl. Ph.D. Thesis, Málaga Univ., Málaga.
- SEARCY, W. A. 1982. The evolutionary effects of mate selection. Ann. Rev. Ecol. Syst. 13:57–85.
- VALVERDE, J. A. 1982. Librea básica y coloración social en el camaleón común, *Chamaeleo chamaeleon* (L.). Publ. Centro Pir. Biol. Exp. 13:55–57.
- VERRELL, P. A. 1985. Male mate choice for larger, more fecund females in the red-spotted newt Notophthalmus viridescens: how is size assessed? Herpetologica 41:382–386.
- . 1994. Males may choose larger females as mates in the salamander *Desmognathus fuscus*. Anim. Behav. 47:1465–1467.

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