Copeia, 2000(2), pp. 610–614

Small Clutch Size in a Mediterranean Endemic Lacertid (*Podarcis milensis*)

C. ADAMOPOULOU AND E. D. VALAKOS

The reproductive strategy of *Podarcis milensis* exhibits some peculiarities when compared with other congeners. Males and females attain sexual maturity at a minimum body size of 47 and 42 mm SVL, respectively, both at an age of about one year. *Podarcis milensis* has a very small clutch size, with a mean of 1.73 and a range of 1–3 eggs, and produces multiple clutches annually. Both sexes exhibit a prolonged reproductive period extending from January to August.

MEMBERS of the family Lacertidae are widespread in the Old World, being distributed over Europe, Africa, and parts of Asia. The family comprises over 230 species which are assigned to about 30 genera (Arnold, 1989). Reproductive traits of European lacertids, especially from the western Mediterranean region, have been well documented by various authors (Pollo and Pérez-Mellado, 1990; Castilla et al., 1991; Carretero and Llorente, 1997), whereas life-history information on lizards occurring in the eastern Mediterranean are poorly known and for only a few species (Chondropoulos and Lykakis, 1983; Valakos, 1990).

In this paper, we describe the unusual reproductive cycle of *Podarcis milensis*, a lizard endemic to the Aegean Archipelago (Greece). This knowledge is valuable for its conservation and protection, since the species is the only small lacertid in the area.

MATERIALS AND METHODS

Species.—*Podarcis milensis* is restricted to the Milos Island group (Milos, Kimolos, Polyaigos, Antimilos, and islets). It is a small but robust lizard with a characteristic blue color pattern in males. The species remains active all year. It is mostly a ground dweller, exhibiting dense populations both in open sandy areas such as sand dunes and in cultivated land.

Study area and climate.—The study area is located in the center of Milos Island (24°22′E, 36°40′N), in a sandy coastal area between the sea and Lake Achivadolimni. Vegetation consists almost entirely of *Thymus* sp. and *Juniperus oxycedrus* ssp. *macrocarpa*. *Podarcis milensis* is extremely abundant and uses the small bushes of the area for shelter. The climate is considered semiarid Mediterranean, with annual rainfall varying from 0 to 200 mm. A dry season exists from May through October. The annual temperature, according to the meteorological station on the island, ranges from 10 C to 26 C (min = 8 , max = 31.5). However, in the study area, the air temperature in summer reaches 37–38 C at midday.

Field and laboratory methods.—A total of 341 adult lizards (218 females and 123 males) were included in the study, all coming from Milos Island. Of these, 182 animals came from museum collections, whereas the remaining 159 came from the study site. After capture, specimens were weighed to the nearest 0.1 g with a Pesola balance and processed immediately. In the laboratory, the following measurements were taken for each specimen: SVL (to 1 mm), longest and shortest axes of the right testis, number and diameter of ovarian follicles and number, length and width of oviductal eggs. Female sexual maturity was assessed by the presence of enlarged vitellogenic follicles (more than 3 mm in diameter) or oviductal eggs, whereas the simultaneous presence of large vitellogenic follicles and oviductal eggs was considered evidence for multiple clutches. The size at sexual maturity for males was estimated by the presence of secondary sexual characters such as the characteristic light blue color of the throat. All field specimens were deposited at the Zoological Museum of the University of Athens. The same measurements were taken for museum specimens previously collected (see Materials Examined). The mean length of the nine eggs deposited in the laboratory was 15.3 mm (range = 14–18, S.D. = 1.11) and the mean width 8.0 mm (range = 7–9, S.D. = 0.64). Only eggs matching or exceeding these parameters were used in estimating egg size and volume from preserved animals. Estimates of testis and egg volume were obtained using the formula for the volume of an ellipsoid.

Age classes for females were determined by the von Bertalanffy equation and were as follows (Adamopoulou, 1999): (1) < 44 mm SVL; (2) $44 \leq$ SVL < 53 mm; (3) $53 \leq$ SVL < 57 mm;

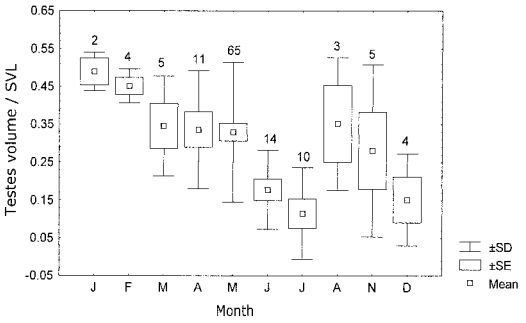

Fig. 1. Annual variation of testis volume: SVL ratio in adult males of *Podarcis milensis*. Sample size is indicated above each month.

and (4) ≥ 57 mm. We determined the time of hatching and SVL of hatchlings in the field by the presence of a ventral navel scar (Galán, 1996).

Comparisons between the two samples (museum and field specimens) were made using analysis of covariance (ANCOVA) with SVL as the covariate. The relationships between clutch size, female body size, and mean egg volume were examined using linear regression analyses, whereas monthly changes in testis/SVL ratio were assessed using analysis of variance (ANOVA).

RESULTS

In general, *P. milensis* males are larger than females. In our sample, the mean SVL for adult males was 56.7 mm (range = 47–68, SD = 4.7, n = 123), and the mean SVL for adult females was 50.4 mm (range = 42–61, SD = 4.42, n = 218).

Testing the two samples.—We found no significant differences between museum and field specimens in clutch size ($F_{(1,123)} = 2.20$, $P > 0.05$), egg length ($F_{(1,59)} = 0.81$, $P > 0.05$), egg width ($F_{(1,79)} = 0.24$, $P > 0.05$), mean egg volume ($F_{(1,53)} = 1.15$, $P > 0.05$), number of large vitellogenic follicles ($F_{(1,26)} = 0.02$, $P > 0.05$), or testis volume ($F_{(1,120)} = 0.5$, $P > 0.05$). Therefore, the two samples were pooled together for further analysis.

Males.—Minimum size at sexual maturity was found to be 47 mm SVL. Testes exhibit their maximum volume in January and February. After a period of stability at slightly smaller sizes from March to May, testes volume decreased in June and reached minimum size in July, with recrudescence beginning in August. A second gradual decrease in testes volume began in November and continued through December, followed by a rapid increase to maximum values in January (Fig. 1). There was a significant difference between months in testes volume/SVL ratio (ANOVA, $F_{(9,113)} = 3.63$, $P < 0.05$).

Females.—The smallest reproductive female measured 42 mm SVL which, according to our estimations, was reached by most females at the age of 12 months. The mean clutch size (based on oviductal eggs) was 1.73 (range = 1–3, SD = 0.64, CV = 0.36, n = 126). The mean second clutch size was 1.27 (range = 1–3, SD = 0.53, n = 29) and was significantly different from the first one (*t*-test, $t = 3.56$, $P < 0.05$). The average egg length was 16.1 mm (range = 14–21, SD = 1.521, CV = 0.09, n = 62) and the average egg width 8.2 mm (range = 7–11, SD = 0.738, CV = 0.09, n = 82). According to our field observations, the first hatchlings appear at the end of April and the last at the end of September. They have an SVL of 24–31 mm.

Females of all age classes did not differ in clutch size ($F_{(3,122)} = 0.927$, $P > 0.05$), number of enlarged vitellogenic follicles ($F_{(2,26)} = 1.551$, $P > 0.05$), or width of oviductal eggs ($F_{(3,78)} = 1.065$, $P > 0.05$). There was a significant difference between age classes in egg length ($F_{(3,58)} = 3.795$, $P < 0.05$); larger females of class 4 carried the longest eggs of all female age classes (Table 1).

In Figure 2, the percentage of sexually ma-

TABLE 1. PERCENTAGE (%) OF SEXUALLY MATURE *Podarcis milensis* FEMALES OF EACH CLASS HAVING 1, 2, OR 3 EGGS PER CLUTCH. Mean SVL, mean clutch size, and mean egg length for each class (with range and SD) are shown in the first three columns. The sample size for each class is given in parentheses.

				Clutch size		
Age class	Mean SVL (mm)	Mean clutch size	Mean egg length (mm)	1	2 (%)	3
I (17)	42.6, (42–3.5), SD = 0.55	1.66, (1–2), SD = 0.57	15, SD = 0	33.3	66.7	—
II (129)	48.6, (44–52), SD = 2.47	1.72, (1–3), SD = 0.58	16.2, (14–20), SD = 1.49	34.7	58.7	6.6
III (54)	54.5, (53–56.5), SD = 1.06	1.77, (1–3), SD = 0.74	15.4, (14–18), SD = 1.12	41	41	18
IV (18)	58.0, (57–61), SD = 1.07	1.66, (1–3), SD = 0.7	18.0, (17–21), SD = 1.77	44.4	44.4	11.2

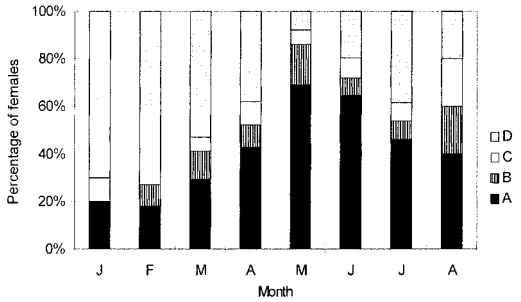

Fig. 2. Seasonal variation in the percentage of sexually mature females in *Podarcis milensis* (n = 218). Females with (A) oviductal eggs, (B) oviductal and large vitellogenic follicles (> 3 mm), (C) large vitellogenic follicles (> 3 mm), (D) without reproductive activity.

ture females with or without reproductive activity is plotted for each month from January onward with a peak in May and a gradual decline toward August. In May, almost 90% of the females in our sample were reproducing.

The smallest females start their reproductive activities in May (Table 2). It seems that they have no second clutch, although this may be due to the small sample examined. Females of the second class, which represents the majority of the population, have large vitellogenic follicles from March onward, whereas we have evidence for further clutches in April to July. The larger females of the third and fourth age class start their reproductive activity in January and end in August. Females of the fourth age class carry eggs from February to August. Beginning in October, all females were reproductively inactive. The simultaneous occurrence of oviductal eggs and enlarged vitellogenic follicles during most months of the reproductive season confirms that at least a proportion of individual females produce at least two clutches per year. There was no significant correlation between clutch size and female SVL ($r = 0.09$, $R^2 = 0.008$, $P > 0.05$) or female SVL and mean egg volume ($r = 0.152$, $R^2 = 0.023$, $P > 0.05$), but mean egg volume was significantly inversely correlated with clutch size ($r = -0.475$, $R^2 = 0.225$, $P < 0.05$).

Discussion

Podarcis milensis, compared to other *Podarcis* species, exhibits an exceptionally small clutch size in combination with the capability of producing more than one annual clutch. Bauwens and Díaz-Uriarte (1997) analyzed patterns of lacertid life-history variation and proposed that species within this clade can be arranged along a single, multivariate axis. *Podarcis milensis* clearly is placed at one end of this continuum as a small-sized species that matures early and has small clutches of relatively large young, multiple broods per year, and a short adult lifespan.

The species displays a prolonged reproductive period extending from January to the end of summer. During both years of this study, large females were seen either pregnant or copulating in January. Males *P. milensis* exhibit a reproductive cycle synchronized with that of females. *Podarcis milensis* is the first European lacertid to our knowledge having such an extensive breeding season and small clutch size. Other Mediterranean *Podarcis* species studied (*P. erhardii*, Naxos Island, Valakos, 1990; *P. taurica*, Ionian archipelago, Chondropoulos and Lykakis, 1983; *P. bocagei*, Iberian peninsula, Galán, 1996; *P. pityusensis*, northeast Spain, Carretero et al., 1995; *P. atrata*, Columbretes islands, Bauwens and Díaz-Uriarte, 1997) have shorter breeding seasons, larger clutch sizes, and larger SVLs at reproductive maturity.

The fact that no significant relationship between SVL and either clutch size or mean egg volume was found implies that *P. milensis* has reached an evolutionarily optimum egg volume and clutch size, showing no increase in the two variables with an increase in body size. The negative correlation between mean egg volume and

Table 2. Reproductive Phenology of Each Female Age Class in *Podarcis milensis*. Reproductive season was estimated by the first and last appearance of oviductal eggs whereas evidence for later clutches was given by the simultaneous presence of oviductal eggs and large vitellogenic follicles. The sample size is given in parentheses.

Female classes	Reproductive season according to the presence of oviductal eggs	Evidence for later clutches
I (17)	May	—
II (129)	April–July	April, May, June, July
III (54)	January–July	April, May, June
IV (18)	January–August	February, March, May, June, August

clutch size may reflect the extent to which female *P. milensis* ''burden'' themselves with eggs. For example, the space available for eggs in the body cavity of females may place an upper limit on their volume (Shine, 1992). To avoid producing nonviable eggs or hatchlings, females must increase egg size at the expense of clutch size.

It seems that for some reason *P. milensis* has evolved a low and quite invariable clutch size, producing large eggs in relation to those of other lacertids for which data are available. Nevertheless, small clutch size may not be an adaptation but the consequence of selection on other life-history parameters such as large offspring size. Larger eggs produce larger young which in turn have a survival advantage over smaller ones (Ferguson and Fox, 1984; Sinervo, 1990). If this is the case in *P. milensis*, high intraspecific competition might increase selection for large eggs with the potential for enhanced offspring survival rather than larger clutch size. Population density at the study site reaches a level of 550–600 animals/ha (Adamopoulou, 1999), which is considered high, the consequences of which are manifested in at least two ways. First, adult males have been seen expressing aggressive behavior toward juvenile males both in the laboratory and in the field, even killing them instantly by neck biting when put together. Second, cannibalism (whole hatchlings in the stomach) has been detected in adult males. Alternatively, the effect of high predation on adult lizards might result in selection for early reproduction (Gadgil and Bossert, 1970), which is associated with small clutch size and more than one clutch per season (Tinkle et al., 1970). Indeed, adult *P. milensis* are exposed to a similar array of predators as are continental species (Pérez-Mellado et al., 1997), including birds of prey and three species of snakes such as the Blunt-Nosed Viper *Macrovipera schweizeri*, 21.4 % of the diet of which consists of *P. milensis* (Adamopoulou et al., 1997).

On the other hand, low clutch number is associated in this species with the potential for frequent ovipositions, which is favored by weather conditions that probably favor the extension of the reproductive season. In winter, individual *P. milensis* take advantage of numerous sunny days to bask, since the air temperature in the sand dune of Achivadolimni reaches 20 C in January and February.

To summarize, we cannot offer a single explanation for the evolution of low clutch size in *P. milensis*. However, considering the ability of the species to produce multiple clutches, the most plausible mechanism for producing more offspring may be to increase clutch frequency, thus spacing clutches temporally and spatially. Selection may have favored the evolution of opportunistic reproductive behavior in females, in which energy is invested not in the number or size of eggs per clutch but in their frequency, thus taking complete advantage of favorable climatic conditions within the constraints of age and physiological state. The extended isolation of the Milos Islands group (since the upper Pleistocene; Papanikolaou and Dermitzakis, 1981) may have enabled *P. milensis* to develop a more efficient reproductive strategy than the other *Podarcis* species of the Aegean with regard to the special climatic conditions of insular Mediterranean-type ecosystems.

Material Examined

Institutional abbreviations are as listed in Leviton et al. (1985). The specimen number is followed by the collecting locality and the month and year of collection as noted on the labels: ZMFK 1657–1711, ZMFK 1742–1801 (Milos, 5/1953), ZMFK 30999–31030 (Milos, 6/1956), NMW 15257:1–15257:29 (Milos, 5/1954), NMW 24035:6–24035:14 (Milos, 7/1979), NMW 11 452:1–11452:11 (Milos, 7/1932).

Acknowledgments

We thank W. Böhme [Herpetological Collection of the Alexander Koenig Zoological Institute and Museum (Bonn, Germany)] and F. Tiedemann and H. Grillitsch (Naturhistorisches Museum of Wien) who kindly allowed us to examine *Podarcis milensis* specimens. We also thank two anonymous reviewers for their useful comments. This study was supported by the General Secretariat for Research and Technology, project 1298/95ED. The collection of specimens was carried out according to Presidential Decree 67/81.

Literature Cited

Adamopoulou, C. 1999. Structure and function of epigeic animal communities with emphasis in the lizard *Podarcis milensis* (Sauria: Lacertidae), in insular ecosystems of the Aegean. Unpubl. Ph.D. diss., Univ. of Athens, Athens, Greece.

———, E. D. Valakos, and A. Legakis. 1997. Notes on the diet and reproduction of the Cyclades blunt-nosed viper *Macrovipera schweizeri* (Werner, 1935). Herpetozoa 10:173–175.

Arnold, E. N. 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old World family of lizards derived from morphology. Bull. Brit. Mus. (Nat. Hist.) 55:209–257.

Bauwens, D., and R. Díaz-Uriarte. 1997. Covariation

of life-history traits in lacertid lizards: a comparative study. Am. Nat. 149:91–111.

CARRETERO, M. A., AND G. A. LLORENTE. 1997. Reproduction of *Psammodromus algirus* in coastal sandy areas of NE Spain. Amphib.-Reptilia 18:369–382.

———, ———, X. SANTOS, AND A. MONTORI. 1995. Características reproductoras de una población introducida de *Podarcis pityusensis*. Rev. Esp. Herpetol. 9:93–102.

CASTILLA, A. M., L. J. BARBADILLO, AND D. BAUWENS. 1991. Annual variation in reproductive traits in the lizard *Acanthodactylus erythrurus*. Can. J. Zool. 70: 395–402.

CHONDROPOULOS, B. P., AND J. J. LYKAKIS. 1983. Ecology of the Balkan wall lizard *Podarcis taurica ionica* (Sauria: Lacertidae) from Greece. Copeia 1983: 991–1001.

FERGUSON, G. W., AND S. F. FOX. 1984. Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. Evolution 38:342–349.

GADGIL, M., AND W. H. BOSSERT. 1970. Life history consequences of natural selection. Am. Nat. 104:1–24.

GALÁN, P. 1996. Sexual maturity in a population of the lacertid lizard *Podarcis bocagei*. Herpetol. J. 6:87–93.

LEVITON, A. E., R. H. GIBBS JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology. Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–821.

PAPANIKOLAOU, D. J., AND M. D. DERMITZAKIS. 1981. The Aegean Arc during Burdigalian and Messinian: a comparison. Riv. Ital. Paleont. 87:83–92.

PÉREZ-MELLADO, V., C. CORTI, AND P. LO CASCIO. 1997. Tail autotomy and extinction in Mediterranean lizards. A preliminary study of continental and insular populations. J. Zool. Lond. 243:533–541.

POLLO, C. J., AND V. PÉREZ-MELLADO. 1990. Biología reproductora de tres especies Mediterráneas de Lacertidae. Mediter. Ser. Biol. 12:149–160.

SHINE, R. 1992. Relative clutch mass and body shape in lizards and snakes: is reproductive investment constrained or optimized? Evolution 46:828–833.

SINERVO, B. 1990. The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Ibid.* 44:279–294.

TINKLE, D. W., H. M. WILBUR, AND S. G. TILLEY. 1970. Evolutionary strategies in lizard reproduction. *Ibid.* 24:55–74.

VALAKOS, E. D. 1990. The ecology of the lizard *Podarcis erhardii* in a typical insular ecosystem on Naxos island. Unpubl. Ph.D. diss., Univ. of Athens, Athens, Greece.

(CA) UNIVERSITY OF ATHENS, DEPARTMENT OF BIOLOGY, ZOOLOGICAL MUSEUM, PANEPISTIMIOUPOLIS 157 84, ATHENS, GREECE; AND (EDV) UNIVERSITY OF ATHENS, DEPARTMENT OF BIOLOGY, SECTION OF ANIMAL AND HUMAN PHYSIOLOGY, PANEPISTIMIOUPOLIS 157 84, ATHENS, GREECE. PRESENT ADDRESS: (CA) BIOLOGY DEPARTMENT, EARTH AND MARINE SCIENCES BUILDING D324, UNIVERSITY OF CALIFORNIA, 1156 HIGH STREET, SANTA CRUZ. CALIFORNIA 95064. E-mail: (CA) chloe@biology.ucsc.edu; and (EDV) evalakos@biology.db.uoa.gr. Send reprint requests to CA. Submitted: 23 Sept. 1998. Accepted: 8 Aug. 1999. Section editor: A. H. Price.