Reproductive Characteristics of the Lacertid Lizard *Podarcis atrata*

Aurora M. Castilla and Dirk Bauwens

We report reproductive characteristics (timing of sexual maturity, clutch frequency, clutch size, egg and hatchling sizes) of the Island Lizard *Podarcis atrata*. Reproductive performance was related to female size. The larger females initiate reproductive activities early in the season and produce two to four clutches annually, whereas the smaller individuals postpone reproduction until the season is well advanced and lay only a single clutch. Clutch size increased with female length and was slightly lower for clutches laid during June–July than for those produced during May. Among-clutch differences in egg mass were negatively correlated with clutch size, and this relationship is independent of female size. Larger clutches are also composed of less elongated (i.e., rounder) eggs than are smaller clutches, suggesting that the phenotypic trade-off between egg size and numbers is induced by limitations posed by the females' body volume, rather than by restrictions of energy availability. Comparison of reproductive traits of *P. atrata* to those of the closely related *P. hispanica* and *P. bocagei* indicates that the increase in body length during the evolutionary divergence of *P. atrata* was not associated with an increase in clutch size. This provides a clear exception to the general pattern found in lacertid lizards.

En este estudio proporcionamos información sobre las características reproductoras (alcance de la madurez sexual, frecuencia de puesta, tamaño de los huevos y de los jóvenes) de la lagartija insular *Podarcis atrata*, en relación con el tamaño de la hembra. Las hembras de mayor tamaño iniciaron su actividad reproductora al comienzo de la temporada, y produjeron entre dos y cuatro puestas al año. Sin embargo, las hembras más pequeñas retrasaron el inicio de su actividad reproductora y sólo realizaron una puesta al año. El tamaño de puesta incrementó con la longitud corporal de la hembra, y fue ligeramente inferior en las puestas realizadas en junio y julio que en las puestas producidas en mayo. Las diferencias entre puestas en el peso del huevo estuvieron negativamente correlacionadas con el tamaño de puesta, independientemente del tamaño de la hembra. Además, en las puestas más grandes, los huevos tenían una forma menos elongada (i.e., redondeados) que en las puestas más pequeñas. Los resultados anteriores sugieren que el "trade-off" entre el tamaño del huevo y de la puesta debe estar inducido por las limitaciones impuestas por el volumen de la hembra, más que por restricciones de disponibilidad de energía. La comparación de las características reproductoras de *P. atrata* con las de otras especies relacionadas, *P. hispanica* y *P. bocagei*, ha indicado que el incremento en la longitud corporal durante la divergencia evolutiva de *P. atrata* no ha estado acompañado de un incremento en el tamaño de puesta. Esto constituye una clara excepción del patrón encontrado en lacértidos.

A N organism's life history is characterized by traits that profoundly affect its fecundity and survival: age and size at maturity; frequency of reproduction; clutch size; size of eggs and hatchlings; and survivorship at different life stages (Roff, 1992; Stearns, 1992). Life-history traits often exhibit considerable variation at different levels: among individuals within the same population; among populations of single species; and among different species. Studies of life-history variation at these different levels address distinct but complementary questions. Studies of single populations focus on proximate causes of variation (e.g., genetic, ontoge-

netic), including environmental factors that induce temporal variation on an ecological time scale (i.e., phenotypic plasticity). On the other hand, interspecific comparisons address the outcome of evolutionary processes and the long-term action of ecological conditions. Although many interspecific comparisons of reptile, especially lizard, life histories are available (e.g., Tinkle et al., 1970; Dunham et al., 1988; Clobert et al., 1998), most authors stressed the need for enlarging and improving the dataset through detailed studies of single species.

Lizards of the family Lacertidae are widespread and abundant in many parts of the Old

World. Despite their conspicuousness, few accounts of their life histories have been published: only 16 of over 230 members of this family (Arnold, 1989) were included in a recent review by Bauwens and Díaz-Uriarte (1997).

We here report a study of reproductive characteristics of *Podarcis atrata*, a species whose world range is restricted to four small islets (total area approximately 20 ha) within the Mediterranean (Castilla and Bauwens, 1991). Knowledge of the reproductive habits of this species is of general interest, considering the paucity of studies dealing with island lizards (except for species of the genus *Anolis*, which all lay a clutch of a single egg; Andrews and Rand, 1974). Our main aims are to: (1) provide detailed quantitative information on the timing of sexual maturity, clutch frequency, clutch size, and egg size and examine individual variation in these traits in relation to female size; (2) analyze the relationship between egg numbers and size and shape of the eggs; (3) compare reproductive traits of *P. atrata* to those of the closely related taxa, *P. hispanica* and *P. bocagei*.

MATERIALS AND METHODS

Species and study area.—*Podarcis atrata* is a small (adult SVL: 50–70 mm), heliothermic and actively foraging lacertid lizard that is endemic to the Columbretes islands (Castilla and Bauwens, 1991). It has long been considered a subspecies of *Podarcis hispanica*, but a recent study using molecular markers (mitochondrial DNA sequences) warranted elevating it to species status (Castilla et al., 1998).

The Columbretes islands constitute an archipelago of small islets of volcanic origin situated in the Mediterranean, approximately 50 km off the coast of Castellón, Spain. This study deals with lizards that inhabit the island Columbrete Grande (39°54′N, 0°41′E), the largest (13 ha) islet of the archipelago. Vegetation on the islets consists mainly of perennial shrubs (*Suaeda vera, Lobularia maritima*), herbs (*Lavatera mauritanica, Malva parviflora*), and patches of grasses. Trees are absent, except for one introduced individual of *Ficus carica*. The archipelago experiences a Mediterranean climate with warm and dry summers and mild winters (mean annual temperature: 17 C; annual rainfall: 265 mm/ year). Most precipitation occurs during autumn. Lizard activity peaks during March–October, although some (juvenile) individuals can be seen during periods of warm and sunny weather in winter.

Data collection.—This report is based on data collected during 1992, 1993, and 1998. We carried out a mark-recapture study during May–July 1992. Lizards were caught with a noose or in baited traps, marked individually by toe-clipping, and released after noting identity, sex, reproductive condition, and snout–vent length (SVL, to nearest 0.1 mm). Sexual maturity was assessed by noting the presence of enlarged follicles or oviductal eggs through palpation of the females' abdomens, the presence of a mating scar (all mated females that were subsequently recaptured proved to be gravid), or the appearance of abdominal skin folds that testify to recent egg-laying. The number of oviductal eggs could be counted by carefully palpating the females' abdomens. The (minimum) number of clutches produced annually was estimated through examining the reproductive condition of individual females over consecutive recaptures.

During 1993, we caught 26 gravid females and kept them in captivity until they had laid their eggs. Individual females were housed in 60 × 20 × 45 cm terraria with a substrate of sand, and stones and leaf litter were provided as sheltering sites. A box with wet sand was provided for egg-laying. The terraria were placed under natural conditions on the island. Food (mealworms) and water were available ad libitum. Females were caught on different dates (from 20 May to 19 July) throughout the reproductive season. Following oviposition, eggs were removed from the terraria, weighed (to nearest 0.01 g) and measured (maximum length and width to nearest 0.1 mm) and, as part of another study, marked individually and incubated in artificial nests (Castilla and Swallow, 1995, 1996). Subsequently females were released so that we obtained a single clutch from each female. Hatchlings from these artificial nests were weighed (to nearest 0.01g) and measured (SVL and tail length; to nearest 0.1 mm) within 24 h.

An additional sample of 10 females and 10 males was caught on 14 April 1998 and transported to the Institute of Nature Conservation (Brussels, Belgium). Pairs of lizards were housed in 100 × 40 × 40 cm terraria with a 5-cm deep substrate of sand; several stones, pieces of bark, and a layer of leaf litter provided shelter. A plastic box filled with wet sand was provided for oviposition. The terraria received natural daylight; a 120 W light bulb, suspended at a height of 30 cm above one end of each terrarium, created a thermal gradient for 9.5 h/ day. Food (crickets and mealworms) and water (periodically supplemented with a vitamin A + D3 mixture) were provided ad libitum. Lizards

initiated mating approximately seven days after arrival in the laboratory and were kept in captivity until September, that is, two months after termination of the reproductive season. Adult lizards and their lab-born progeny were then shipped back to Columbretes and released.

We inspected gravid females at least once daily. Following oviposition, the female was weighed, and the eggs were removed, weighed (to nearest 0.01 g), measured (maximum length and width; to nearest 0.1 mm), and their viability was judged by the presence of an embryonic disc (indicative of fertilization) and external characteristics of the eggshell. As part of another experiment, the eggs were incubated individually at different temperature regimes. Hatchlings were weighed (to nearest 0.01g) and measured (SVL and tail length; to nearest 0.1 mm) within 24 h. Eggs that did not hatch were dissected; the developmental stage of the embryo was determined according to the table of Dufaure and Hubert (1961).

Data analyses.—To examine temporal variation in clutch size within a reproductive season, we distinguished between two periods: May–14 June (hereafter named ''May'') and 15 June–July (''June–July''). These correspond approximately to when the first (and part of the second) clutches and the later clutches are laid in this population.

Clutch mass was calculated as the sum of the masses of all eggs in each clutch. Relative clutch mass was estimated by the ratio between clutch mass and the mass of the female after laying. We calculated relative egg length, an estimate of degree of elongation (i.e., shape) of the eggs, as the logarithm of the ratio between egg length and egg width.

We used multiple regression to examine the relationship between egg characteristics (i.e., mass, length, width, relative egg length) and clutch size, while holding female SVL constant (all variables were log-transformed prior to analyses). However, estimates of the partial regression coefficients may be biased when the independent variables (i.e., clutch size and female SVL) are highly correlated (''multicollinearity,'' Slinker and Glantz, 1985). To avoid such artifacts, we first calculated residual clutch size by computing the residuals from the least-square regression of clutch size on female SVL. Residual clutch size and female SVL, which are by definition uncorrelated, were then used as independent variables in the multiple regression analyses.

RESULTS

Sexual maturity.—The smallest reproductive female had a SVL of 51 mm, whereas all females with a SVL $\geq$ 59 mm were reproductive. The percentage of females with a SVL of 51–58 mm that were reproductive was lower during May 1992 (7 of 26, 27%) than during June–July 1992 (15 of 18, 83%; $\chi^2 = 13.5$, 1 df, $P < 0.001$). Hence, an important fraction of the smaller females initiate reproductive activities one to two months later than the larger females.

Clutch frequency.—Successive recaptures of marked individuals during the 1992 field season revealed that individual females produced 1–3 clutches. Females that produced only a single clutch had a smaller SVL (mean $\pm$ 1 SE = 62.2 $\pm$ 0.6 mm, n = 46) than females laying 2–3 clutches (64.9 $\pm$ 0.5 mm, n = 31; Mann-Whitney U-test, $P < 0.01$).

Females kept in the laboratory during 1998 laid 1–4 clutches (2, 1, 4, and 3 females produced 1, 2, 3, and 4 clutches, respectively). Lizards that laid 1–2 clutches were on average smaller (61.0 $\pm$ 1.0 mm, n = 3) than those producing 3–4 clutches (64.2 $\pm$ 0.8 mm, n = 7; Mann-Whitney U-test, $P = 0.05$).

Clutch size.—The number of eggs in a clutch varied from 1–5, but the vast majority (97% of n = 152) of the clutches were composed of 2–4 eggs. Clutch size increased with SVL ($r = 0.40$, $P < 0.001$). We used a mixed-model ANCOVA (Type III SS) to assess the effects of year (random factor) and period (fixed factor) on clutch size (log-transformed), with SVL (log-transformed) as the covariate. Slopes of the regression equations between clutch size and SVL for each period and year were not significantly heterogeneous ($F_{2,145} = 0.21$, $P > 0.80$). Clutch size, adjusted for SVL, did not differ significantly among years ($F_{2,147} = 3.00$, $P > 0.05$), but there was a marginally significant difference between periods ($F_{2,147} = 4.03$, $P = 0.046$). During all years, adjusted clutch size was slightly higher during May than in June–July (Table 1).

Clutch mass and relative clutch mass.—Clutch mass (summary statistics in Table 2), increased with adult female SVL ($r = 0.371$, $P < 0.01$). The slope of this relationship (b = 1.862; SE = 0.673; log-log transformed data) does not differ significantly from the expected value (= 3) under a model of geometric similarity ($t = 1.691$, $P = 0.10$). Relative clutch mass is not correlated with female length ($r = 0.119$, $P > 0.50$). Thus,

TABLE 1. SUMMARY STATISTICS (MEAN ± 1SE) FOR CLUTCH SIZE AND SNOUT-VENT LENGTH OF REPRODUCTIVE FEMALE *Podarcis atrata* AND ADJUSTED MEAN CLUTCH SIZE IN DIFFERENT YEARS AND PERIODS.

		Clutch Size	SVL (mm)	Adjusted Clutch Size	n
1992	May	2.9 ± 0.1	63.6 ± 0.5	2.8	70
	June–July	2.5 ± 0.1	62.1 ± 0.8	2.5	32
1993	May	3.0 ± 0.2	62.1 ± 1.1	3.1	11
	June–July	3.0 ± 0.3	62.4 ± 1.0	3.0	14
1998	May	3.1 ± 0.2	63.6 ± 0.6	3.1	16
	June–July	2.9 ± 0.4	63.4 ± 0.8	2.8	9
Total		2.8 ± 0.1	63.0 ± 0.3		152

clutch mass increases in direct proportion to female size.

Egg and hatchling size.—A significant proportion of the total variation in all measures of egg size and shape (mass, length, width, relative egg length; summary statistics in Table 2) was attributable to differences among clutches (one-way ANOVAs, all $P < 0.001$). Therefore, average values for each clutch were used in all following analyses.

Mean egg mass in a clutch decreased significantly with clutch size ($r = -0.552$, $P < 0.001$) and residual clutch size ($r = -0.596$, $P < 0.001$) but was not correlated with female SVL ($r = 0.084$, $P > 0.90$). Hence, larger clutches are composed of smaller eggs, independent of female SVL.

We next examine whether the decrease in egg mass with increasing egg numbers is associated with equivalent changes in linear egg dimensions (i.e., width and length of the eggs) or, alternatively, with a change in egg shape. Both mean egg width and mean egg length for a clutch decreased with residual clutch size (width: $r = -0.307$, $P < 0.05$; length: $r = -0.625$, $P < 0.001$) and with clutch size (width: $r = -0.239$, $P < 0.05$; length: $r = -0.618$, $P < 0.001$). This is hardly surprising given the decrease of egg mass with (residual) clutch size

and the positive correlations between egg mass and egg width ($r = 0.785$, $P < 0.001$) and egg length ($r = 0.762$, $P < 0.001$). Nevertheless, relative egg length (i.e., the logarithm of the length/width ratio), which is not correlated with egg mass ($r = 0.233$, $P > 0.10$), decreases significantly with residual clutch size ($r = -0.415$, $P < 0.005$) and clutch size ($r = -0.454$, $P < 0.005$), indicating that an increase in egg numbers is associated with the production of less elongated eggs. Moreover, when we statistically control for the variation in egg mass by partial correlation, increases in residual and absolute clutch size are significantly associated with increases in egg width (residual clutch size: $r = 0.324$, $P < 0.05$; clutch size: $r = 0.377$, $P < 0.01$) but with decreases in egg length (residual clutch size: $r = -0.328$, $P < 0.05$; clutch size: $r = -0.365$, $P < 0.01$) and relative length (residual clutch size: $r = -0.354$, $P < 0.02$; clutch size: $r = -0.401$, $P < 0.01$). Thus, at a given egg mass, eggs in large clutches are wider and shorter (both absolutely and relatively) than those from smaller clutches. Mean mass of hatchlings in a clutch was positively correlated with mean mass of the eggs ($r = 0.700$, $P < 0.001$).

Hatching success.—Detailed data on hatching success are available for the 1998 laboratory study only. Of a total 75 eggs judged to be viable

TABLE 2. SUMMARY STATISTICS FOR MEASUREMENTS OF EGG AND HATCHLING SIZE, AND CLUTCH MASS AND RELATIVE CLUTCH MASS IN *PODARCIS ATRATA*. SE = standard error of the mean; n = number of eggs, hatchlings, or clutches.

	Mean	SE	Min	Max	n
Egg mass (g)	0.37	0.01	0.26	0.71	104
Egg length (mm)	12.4	0.1	10.1	15.6	104
Egg width (mm)	7.3	0.1	6.3	8.9	104
Hatchling mass (g)	0.52	0.01	0.43	0.73	55
Hatchling SVL (mm)	29.0	0.2	26.5	31.5	31
Clutch mass (g)	1.14	0.04	0.71	1.85	51
Relative clutch mass	0.241	0.011	0.146	0.367	25

at oviposition from 25 clutches, 40 eggs (53%) hatched. All but one of the eggs that did not hatch had fully developed embryos (developmental stage 40) that had seemingly been unable to split the eggshell. The remaining egg did not contain an embryo. Hatching success of *P. atrata* eggs was clearly lower than for eggs of *P. hispanica* (72 of 95, 76%) that were incubated concurrently and under the same conditions of temperature and moisture in the laboratory.

Hatching success of *P. atrata* eggs that were judged viable at oviposition differed dramatically among individual clutches ($G = 96.00$, df $= 24$, $P < 0.001$). All eggs from 13 clutches and two out of three eggs from two other clutches hatched, whereas 10 clutches were entirely composed of eggs that failed to hatch. The distribution of clutches that did or did not contain eggs that hatched was nonrandom among the different females ($G = 20.47$, df $= 9$, $P < 0.02$). Four females produced a total of 11 clutches (1–4 clutches per female) with eggs that hatched, three females laid four clutches (1–2 clutches per female) entirely composed of eggs that failed to hatch, whereas three females produced four clutches with eggs that hatched and six clutches of which no eggs hatched.

Comparison with populations of Podarcis hispanica and Podarcis bocagei.—We examined to what extent reproductive characteristics of *P. atrata* diverge from those in populations of the closely related *P. hispanica* and *P. bocagei* (Table 3). Data were available for several populations of *P. hispanica* that mutually differ in average body length, and body size has a pervasive influence on reproductive characteristics. We, therefore, calculated the regression equations between each trait of interest and mean adult female SVL for populations of *P. hispanica*. The equations were then used to calculate the predicted value of each trait, and its 95% prediction interval, at the average female length of *P. atrata*. If the observed value of *P. atrata* fell outside the prediction interval, we rejected the null hypothesis of no divergence between *P. atrata* and *P. hispanica*. We note that, in the absence of information on the relationships among the *P. hispanica* populations, our analysis is unavoidably nonphylogenetic. The failure to incorporate phylogenetic information in comparative analyses may lead to biased estimates of correlation and regression coefficients (Garland et al., 1992) and, hence, of the 95% prediction interval. Nevertheless, we are confident that analytical imperfections have not altered our major results and conclusions.

Observed body length at maturity and egg

TABLE 3. REPRODUCTIVE CHARACTERISTICS OF Podarcis atrata AND DIFFERENT POPULATIONS OF Podarcis hispanica AND Podarcis bocagei. The observed value for *P. atrata* is compared to the predicted value, and the 95% prediction interval, obtained from regression equations for *P. hispanica* (see text for details).

Species/Location	Mean SVL (mm)	SVL at maturity (mm)	Clutch size	Egg mass (g)	Clutch mass (g)	Reference
P. atrata						
observed	63.1	51.0	2.8	0.37	1.14	this study
predicted		52.1	4.0	0.35	1.37	
95% prediction interval		44.8–59.3	3.3–4.8	0.27–0.43	1.12–1.61	
P. hispanica						
Asturias	49.6	39.4	2.1	0.27	0.58	Braña 1983, Braña et al. 1991
Sierra de Gredos	50.4	43.9	2.6			Gil 1992
Sistema Central	50.6	44.0	2.5			Pérez-Mellado 1982
Madrid	56.7	46.3	3.0	0.33	1.01	D. Bauwens, unpubl.
Sierra Guadarrama	57.1	49.4	3.6			García-Fernández 1990
Salamanca	61.3	50.0	3.6	0.34	1.22	D. Bauwens, unpubl.
San Sebastian	61.6		4.0	0.33	1.32	Braña et al. 1991
P. bocagei	55.4	44.0	4.1	0.26	1.02	Galán 1997

mass of *P. atrata* were within the range of values predicted for *P. hispanica*, based upon extrapolation to mean adult female SVL equal to that for *P. atrata* (Table 3). By contrast, observed clutch size for *P. atrata* was significantly lower (by >1 egg) than for *P. hispanica* with similar SVL. As a consequence of the lower clutch size, clutch mass, which is the product of clutch size and egg mass, was lower in *P. atrata*, although the observed value only bordered the lower limit of the prediction interval (Table 3).

Data were available for one population of *P. bocagei* (Table 3), precluding an analysis that accounts for differences in adult female SVL. Adult female *P. bocagei* were significantly smaller but exhibited a larger clutch size and laid smaller eggs than did *P. atrata* (*t*-tests, all $P < 0.001$).

DISCUSSION

Our study reveals three aspects of the reproductive biology of *P. atrata*, which are likely to be of general interest to reptile biologists. These are the observed change in reproductive performance with female size, the trade-off between egg numbers and egg size and shape, and the evolutionary divergence in some reproductive traits between *P. atrata* and the closely related *P. hispanica* and *P. bocagei*. We will discuss these aspects in turn.

Reproductive output and female body size.—Female *P. atrata* initiate reproductive activities at body sizes of 51–58 mm SVL, attained during their first year of life. However, some first-year females, which had attained a SVL of 45–53 mm in June–July, were nonreproductive and presumably delayed maturity until the next year. These observations suggest that sexual maturity is associated with attaining a minimum body size, rather than a minimum age as has been suggested for other lacertids (Heulin, 1985; Bauwens and Verheyen, 1987; Galán, 1996).

A large fraction of the smaller females that had surpassed the minimum length at maturity during May (i.e., with a SVL of 51–59 mm) postponed initiation of reproductive activities until the second half of June or later, whereas the larger females were reproductive from May onward. Hence, larger females initiated reproductive activities before smaller individuals. Similar findings have been reported in the lacertids *L. vivipara* (Bauwens and Verheyen, 1985), *Podarcis bocagei* (Galán, 1996), and *L. agilis* (Olsson and Shine, 1997). These trends are hypothesized to reflect size-related differences in the amount of fat stores. The larger females have more fat stores upon emerging from hibernation (Avery,

1974), enabling them to assimilate or mobilize energy for clutch production at a faster rate and, hence, initiate reproduction earlier than the smaller females (Bauwens and Verheyen, 1985; Olsson and Shine, 1997). Thus, we suggest that it is not only the attainment of a minimum size that induces sexual maturity but that other factors, such as lipid quantities (Hahn and Tinkle, 1965) and/or hormone levels (Ho et al., 1982), are also important determinants.

Our results indicate that female *P. atrata* may produce multiple clutches per year, as do other species of the genus *Podarcis* (e.g., Barbault and Mou, 1988; Galán, 1997). However, the number of clutches laid per year is not a fixed characteristic but differs among individual females, depending at least in part on their body size. Large females, which initiate reproductive activities early in the season, produce two to four clutches annually. On the other hand, the smallest individuals postpone reproduction until the season is well advanced and lay only a single clutch.

Although variation in clutch size was rather restricted (most clutches were composed of 2–4 eggs), a significant portion of the existing variation was related to differences in female length. An increase in egg numbers with female size is a general phenomenon in lacertid lizards (e.g., Bauwens and Verheyen, 1987; Barbault and Mou, 1988; Braña, 1996) and in many other lizards with variable clutch size (e.g., Dunham et al., 1988). An additional portion of the variation in clutch size was attributable to seasonal differences: the number of eggs, adjusted for female length, was slightly but significantly lower for clutches laid during June–July than for those produced during May. A similar decline in clutch size as the reproductive season progresses has been observed in other lacertids (Barbault and Mou, 1988; Heulin et al., 1994; Galán, 1997). Seasonal variation in clutch size presumably reflects differences in the proximate source of the energy allocated to different clutches. In several lacertids, yolk production for the first annual clutch is mainly derived from fat reserves stored before hibernation, whereas energy shunted to subsequent clutches is mainly derived from recent food intake (Braña et al., 1992).

Trade-off between clutch size and egg size.—A central tenet of life-history theory is that increases in offspring size are accompanied by decreases in clutch size (e.g., Lack, 1967; Smith and Fretwell, 1974; Stearns, 1992). This trade-off is inevitable for single reproductive events, given a fixed amount of energy allocated to each one. The

maternal energy allocation may be limited by energy availability or by the volume of the maternal body cavity that contains the eggs (Roff, 1992). Nevertheless, individual differences in energy allocation to reproduction may blur the phenotypic manifestation of the trade-off function (Partridge and Sibly, 1991). Our data show that among-clutch differences in egg mass are negatively correlated with clutch size, and that this relationship is independent of female size. Hence, a trade-off between egg size and numbers is apparent among individual females within the studied population.

Our analyses also demonstrate a relationship between clutch size and egg shape; at a given egg mass, larger clutches are composed of less elongated (i.e., rounder) eggs than are smaller clutches. Under the assumption that resource acquisition limits the amount of energy allocated to reproduction, we expect a negative relationship between egg numbers and egg size but no relationship with egg shape. In contrast, if body volume constrains reproductive allocation, both egg size and egg elongation should decrease with egg numbers. Indeed, for eggs that are arranged linearly in the oviduct, the length of the oviduct should limit egg length (Ford and Seigel, 1989) such that a larger number of eggs can only be accommodated when egg length is reduced. Thus, the observed decrease of egg elongation with clutch size indirectly suggests that reproductive allocation and the resulting phenotypic trade-off between egg size and numbers is induced by limitations imposed by female body volume, rather than by restrictions of energy availability. Qualls and Shine (1995) and Qualls and Andrews (1999) provide other types of evidence for a restriction of reproductive output and egg dimensions by maternal body volume in lizards.

Evolutionary divergence in reproductive traits among Podarcis atrata, Podarcis hispanica, and Podarcis bocagei.—*Podarcis atrata* had long been considered a subspecies of *P. hispanica* and was only recently elevated to species status (Castilla et al., 1998). Thus, based on traditional taxonomy, *P. atrata* and *P. hispanica* should be considered as sister taxa. However, a recent analysis of the phylogenetic relations within *Podarcis* using mitochondrial DNA sequences (Harris and Arnold, 1999) challenges this view. According to this study, *P. atrata* would be more closely related to *P. bocagei* of northwest Iberia than to *P. hispanica*, which inhabits most of the Iberian peninsula including the coast of eastern Spain proximal to the Columbretes Islands. Nevertheless, evidence for this dichotomy pattern is weak, with low

bootstrap support (Harris and Arnold, 1999). Given the conflicts between arguments based on traditional taxonomy, biogeography, and molecular phylogeny, we conservatively consider the phylogenetic relationships among these three species as unresolved. We note that the evolutionary divergence between *P. atrata* and either *P. hispanica* or *P. bocagei* took place within a period of one million years or less, the estimated age of the Columbretes Islands (Martí et al., 1992).

Female *P. atrata* exhibit a larger mean body length than populations of *P. hispanica*. The body length at sexual maturity and egg mass of *P. atrata* are within the range of values expected for a hypothetical population of *P. hispanica* with mean adult female SVL equal to that observed for *P. atrata*. In contrast, clutch size in *P. atrata* is clearly lower than expected for *P. hispanica*, to the extent that absolute numbers of eggs are lower (by more than one egg) than in many populations of *P. hispanica*. Similarly, although adult females of *P. atrata* are clearly larger than female *P. bocagei*, clutch size is considerably smaller (by more than one egg) in the former species. Thus, we hypothesize that the evolutionary divergence of *P. atrata* was characterized by an increase in adult female length but that clutch size either remained constant or, more likely, decreased.

A recent phylogenetically based comparative study explored patterns of covariation among life-history traits in European lacertid lizards (Bauwens and Díaz-Uriarte, 1997). A major conclusion was that evolutionary changes in adult female length were associated with parallel changes in size at sexual maturity, clutch size, egg size, and hatchling length. The increase in female length during the divergence of *P. atrata* without a concomitant increase in clutch size, provides a clear exception to this general pattern.

If species are to persist over time, an evolutionary decrease in clutch size should be compensated for by a change in some other life-history trait. This could be achieved by starting to reproduce at a smaller size (i.e., earlier), by increasing the number of clutches produced annually or by an increase in immature and/or adult survival rates. Available information does not indicate that *P. atrata* starts reproducing earlier, or reproduces more frequently, than *P. hispanica* or *P. bocagei*. Neither is there any evidence for a higher survival rate in the immature life stages. Size of the eggs and hatchlings, which may be associated with higher survivorship (Sinervo et al., 1992), is not disproportionally larger in *P. atrata*, whereas hatching success

in laboratory conditions was lower than in *P. hispanica*. In addition, hatchlings *P. atrata* are subject to frequent cannibalistic attacks by adult conspecifics (Castilla and Van Damme, 1996), but we are unaware of observations testifying cannibalism in populations of *P. hispanica* and *P. bocagei*. Thus, if anything, available information suggests that survival of immature *P. atrata* may be lower than in *P. hispanica* and *P. bocagei*. By contrast, many species of birds and all mammals and snakes that prey on *P. hispanica* and *P. bocagei* on the Iberian mainland are absent from the insular environment inhabited by *P. atrata*, suggesting that predation rate is relaxed on adults (Van Damme et al., 1998). Future studies should nevertheless establish to what extent adult survival rates differ among *P. atrata, P. hispanica*, and *P. bocagei*.

LITERATURE CITED

ANDREWS, R. M., AND A. S. RAND. 1974. Reproductive effort in anoline lizards. Ecology 55:1317–1327.

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. (Zool.) 55:209–257.

AVERY, R. A. 1974. Storage lipids in the lizard *Lacerta vivipara*: a quantitative study. J. Zool. (Lond.) 173: 419–425.

BARBAULT, R., AND Y.-P. MOU. 1988. Population dynamics of the common wall lizard, *Podarcis muralis*, in southwestern France. Herpetologica 44:38–47.

BAUWENS, D., AND R. DíAZ-URIARTE. 1997. Covariation of life-history traits in lacertid lizards: a comparative study. Am. Nat. 149:91–111.

———, AND R.F. VERHEYEN. 1985. The timing of reproduction in the lizard *Lacerta vivipara*: differences between individual females. J. Herpetol. 19:353–364.

———, AND ———. 1987. Variation of reproductive traits in a population of the lizard *Lacerta vivipara*. Holarc. Ecol. 10:120–127.

BRAÑA, F. 1983. La reproducción de los saurios de Asturias (Raptilia; Squamata): ciclos gonadales, fecundidad y modalidades reproductoras. Rev. Biol. Univ. Oviedo 1:29–50.

———. 1996. Sexual dimorphism in lacertid lizards: male head increase vs female abdomen increase? Oikos 75:511–523.

———, A. BEA, AND M. J. ARRAYAGO. 1991. Egg retention in lacertid lizards: relationships with reproductive ecology and the evolution of viviparity. Herpetologica 47:218–226.

———, F. GONZÁLEZ, AND A. BARAHONA. 1992. Relationship between ovarian and fat body weights during vitellogenesis for three species of lacertid lizards. J. Herpetol. 26:515–518.

CASTILLA, A. M., AND D. BAUWENS. 1991. Observations on the natural history, present status, and conservation of the insular lizard *Podarcis hispanica atrata* on the Columbretes archipelago, Spain. Biol. Conserv. 58:69–84.

———, AND J. G. SWALLOW. 1995. Artificial egg-laying sites for lizards: a conservation strategy. Biol. Conserv. 72:387–391.

———, AND ———. 1996. Thermal dependence of incubation duration under a cycling temperature regime in the lizard, *Podarcis hispanica atrata*. J. Herpetol. 30:247–253.

———, AND R. VAN DAMME. 1996. Cannibalistic propensities in the lizard *Podarcis hispanica atrata*. Copeia 1996:991–994.

———, V. FERNÁNDEZ-PEDROSA, D.J. HARRIS, A. GONZÁLEZ, A. LATORRE, AND A. MOYA. 1998. Mitochondrial DNA divergence suggests that *Podarcis hispanica atrata* (Squamata: Lacertidae) from the Columbretes Islands merits specific distinction. *Ibid.* 1998: 1037–1040.

CLOBERT, J., T. GARLAND, AND R. BARBAULT. 1998. The evolution of demographic tactics in lizards: a test of some hypotheses concerning life history evolution. J. Evol. Biol. 11:329–364.

DUFAURE, J. P., AND J. HUBERT. 1961. Table de développement du lézard vivipare: *Lacerta (Zootica) vivipara* Jacquin. Arch. Anat. Micr. Morph. Exp. 50: 309–328.

DUNHAM, A. E., D. B. MILES, AND D. N. REZNICK. 1988. Life history patterns in squamate reptiles, p. 441–522. *In:* Biology of the Reptilia. Vol. 16. Ecology B. Defense and life history. C. Gans and R. B. Huey (eds.). Alan R. Liss, Inc., New York.

FORD, N. B., AND R. A. SEIGEL. 1989. Relationships among body size, clutch size, and egg size in three species of oviparous snakes. Herpetologica 45:75–83.

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

———. 1997. Reproductive ecology of the lacertid lizard *Podarcis bocagei*. Ecography 20:197–209.

García-Fernández, J. 1990. Dieta y reproducción de *Podarcis hispanica* y *Podarcis muralis* en la Sierra de Guadarrama. Unpbul. master's thesis, Universidad de Salamanca, Salamanca, Spain.

Garland Jr., T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst. Biol. 41:18–32.

Gil, M. J. 1992. Estudio de la comunidad de Saurios de la vertiente meridional de la Sierra de Gredos. Unpubl. Ph.D. diss., Universidad de Salamanca, Salamanca, Spain.

Hahn, W. E., and D. W. Tinkle. 1965. Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard *Uta stansburiana*. J. Exp. Zool. 158:79–85.

Harris, D. J., and E. N. Arnold. 1999. Relationships of wall lizards, *Podarcis* (Reptilia: Lacertidae) based on mitochondrial DNA sequences. Copeia 1999: 749–754.

Heulin, B. 1985. Maturité sexuelle et âge à la première reproduction dans une population de plaine de *Lacerta vivipara*. Can. J. Zool. 63:1773–1777.

———, K. Osenegg, and D. Michel. 1994. Survie et incubation des oeufs dans deux populations ovipares de *Lacerta vivipara*. Amphib.-Reptilia 15:199–219.

Ho, S.-M., S. Kleis, R. McPherson, G. J. Heisermann, and I. P. Callard. 1982. Regulation of vitellogenesis in reptiles. Herpetologica 38:40–50.

Lack, D. 1967. The natural regulation of animal numbers. Oxford Univ. Press, Oxford.

Martí, J., J. M. Mitjavila, E. Roca, and A. Aparicio. 1992. Cenozonic magnetism of the Valencia through (westren Mediterranean): relationships between structural evolution and volcanism. Tectonophysics 203:145–165.

Olsson, M., and R. Shine. 1997. The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. J. Evol. Biol. 10:369–381.

Partridge, L., and R. Sibly. 1991. Constraints in the evolution of life histories. Proc. R. Soc. Lond. B Biol. Sci. 332:3–13.

Pérez-Mellado, V. 1982. Algunos datos sobre la reproducción de dos especies de Lacertidae (Sauria, Reptilia) en el Sistema Central. Bol. R. Soc. Española Hist. Nat. (Biol.) 80:165–173.

Qualls, C. P., and R. M. Andrews. 1999. Maternal body volume constrains water uptake by lizard eggs in utero. Funct. Ecol. 13:845–851.

———, and R.Shine. 1995. Maternal body-volume as a constraint on reproductive output in lizards: evidence from the evolution of viviparity. Oecologia 103:73–78.

Roff, D. A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York.

Sinervo, B., P. Doughty, R. B. Huey, and K. Zamudio. 1992. Allometric engineering: a causal analysis of natural selection on offspring size. Science 258: 1927–1930.

Slinker, B. K., and S. A. Glantz. 1985. Multiple regression for physiological data analysis: the problem of multicollinearity. Am. J. Physiol. 249:R1–R12.

Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. Am. Nat. 108:499–506.

Stearns, S. C. 1992. The evolution of life histories. Oxford Univ. Press, Oxford.

Tinkle, D. W., H. M. Wilbur, and S. G. Tilley. 1970. Evolutionary strategies in lizard reproduction. Evolution 24:55–74.

Van Damme, R., P. Aerts, and B. Van Hooydonck. 1998. Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards. Biol. J. Linn. Soc. 63:409–427.

(AMC) Department of Biology, University of Antwerp (U.I.A.), Universiteitsplein 1, B-2610 Wilrijk, Belgium, and Centre Tecnologic Forestal de Catalunya, Puiada del Seminari s/n E-25280 Solsona, Lleida, Spain; and (DB) Institute of Nature Conservation, Kliniekstraat 25, B-1070 Brussel, Belgium. E-mail: (AMC) castilla@uia.ua.ac.be; and (DB) dirk.bauwens@instnat.be. Send reprint requests to DB. Submitted: 26 July 1999. Accepted: 18 Nov. 1999. Section editor: A. H. Price.