Reproductive Characteristics of an Insular Population of the Lizard *Podarcis hispanica* from Northwest Spain (Cíes Islands, Galicia)

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Here I report on the reproductive characteristics of an insular population of the lacertid lizard Podarcis hispanica, which inhabits the Cies Islands, an archipelago formed by three small islands off the northwest coast of Spain. The clutch characteristics of the population were investigated on the basis of clutches laid by pregnant females captured on these islands in 1999 and 2000. Other data were obtained principally by mark-recapture experiments. The egg-laying cycle of live females was determined by ventral palpation. Enlarged follicles were detected from March to July, and the laying period extended from April to the second half of July. The larger females initiated reproductive activities early in the season and produced up to three clutches annually, whereas the smaller individuals laid only a single clutch. Reproductive performance was related mainly to female size. Clutch size, individual egg mass, clutch mass, and hatchling size increased with the length of the females. I also examined the extent to which the reproductive characteristics of this insular population of P. hispanica diverged from those in other populations of the same species. I found no pronounced differences between these populations and other mainland populations of the same species of like body size. Several hypotheses may be proposed to explain the lack of major differences in reproductive characteristics (egg size and number). The first has to do with the relatively short length of time that this population has been isolated, and, therefore, it would still be too early for any divergence to have manifested itself. A second hypothesis is that the selection gradient for reproductive traits on the Cíes Islands may have remained similar to that on the mainland. A third hypothesis deals with the limitations imposed by the reduced body volume of this small-sized species on egg growth in conjunction with the shorter laying period of this population in an Atlantic climate.

A MONG the numerous microevolutionary patterns and processes occurring on islands, there are descriptions of changes in the clutch size of lizards (e.g., Grant, 1998). Clutch sizes of island lizards are small compared with those of their mainland relatives (Kramer, 1946; Case, 1983). However, this trend, which has also been reported in other island terrestrial vertebrates (e.g., Grant and Grant, 1989), has not been studied as thoroughly or on a wide enough systematic scale to be able to verify the consistency of this evolutionary pattern.

In recent years, several studies on the reproductive traits of insular populations of lacertid lizards of the genus *Podarcis* have been published, mainly on species such as *Podarcis pityusensis* (Carretero et al., 1995), *Podarcis atrata* (Castilla, 1996; Castilla and Bauwens, 2000a), and *Podarcis lilfordi* (Castilla and Bauwens, 2000b) that are endemic to the Mediterranean islands. Still, life-history information on insular populations belonging to continental species is much scarcer (e.g., *Podarcis carbonelli berlengensis*, Vicente, 1989, formerly *Podarcis bocagei berlengensis*). These kinds of studies are needed to provide a foundation for comparative analyses on

reproductive characteristics between insular and mainland populations of the same species. Such studies will be able to shed light on the conditioning factors imposed by insularity on the reproductive characteristics in populations having a close phylogenetic relationship (Bauwens, 1999).

In lizard species, a general trend supported by a number of descriptive accounts on life-history traits shows that, when island populations have been isolated for a very long time (≥ 1 million years), major changes take place in their reproductive characteristics, which affect, at the very least, the number and size of the eggs: the lizards lay fewer eggs of a much bigger size (Rodríguez-Domínguez and Molina-Borja, 1998; Castilla and Bauwens, 2000a; Adamopoulou and Valakos, 2000). However, there is much less information on whether these changes occur in lizard populations that have been isolated for a much shorter period (only several thousand years) and belong to the same species as the populations living on the mainland.

In this paper, I describe the reproductive characteristics of an insular population of the lacertid lizard *Podarcis hispanica* from the Cies Islands, an archipelago formed by three relatively small islands off the southwest coast of Galicia, in northwest Spain.

The aim of this study was to determine whether the insular isolation of this population of *P. hispanica*, only a few thousand years old, has resulted in changes in the major reproductive characteristics, particularly egg size and number, in comparison with the mainland populations of the same species.

MATERIALS AND METHODS

Study area.—The Cícs Islands are an archipelago formed by three islands: Monteagudo (182 ha, maximum altitude: 176 m), Faro (106 ha, maximum altitude: 193 m), and San Martiño (146 ha, maximum altitude: 179 m), situated in the Atlantic Ocean, at the mouth of the Ría de Vigo, 2.5 km off the nearest coast, in Pontevedra, northwestern Spain (42°15′N, 8°53′W; UTM 29T NG 07). Monteagudo and Faro are now connected by a cement bridge.

They are continental islands, which broke off from the adjacent coast because of rising sea levels and phenomena of coastal erosion roughly between 8000 and 9000 years ago (according to data extracted from the current sea depths between these islands and the coast and the sea level rise curve, which traces the evolution of the coast line from the last glacial maximum to the present; Dias et al., 2000). It is therefore considered that the nonflying fauna inhabiting these islands at the present time became isolated during that period, except for recent introductions by humans. These phenomena of recent introductions do not appear to have included reptiles (unpubl.).

Vegetation on the islands consists mainly of scrubs (*Ulex europaeus, Cistus salvifolius*), herbs (*Armeria pubigera, Angelica pachycarpa*, etc.), grasses (*Briza media, Dactylis glomerata*, etc.) and woods from reforestation of imported trees, *Eucalyptus globulus* and *Pinus pinaster*. In some limited areas, there are small relict patches of the original woods of Pyrenean oak (*Quercus pyrenaica*).

The insular reptile fauna is composed of five lizard species (Anguis fragilis, Chalcides bedriagai, Chalcides striatus, Lacerta lepida, and P. hispanica), and two snakes (Coronella girondica and Natrix maura). The main predators of P. hispanica on the islands are domestic and feral cats (Felis catus), lizard-eating snakes Coronella girondica, kestrels (Falco tinnunculus), and perhaps rats (Rattus rattus). It is interesting to note that, on the mainland near these islands, P. hispanica lives in sympatry with the related species P. bocagei; yet

on the Cíes Islands, it is the only species of *Podarcis* found (Galán and Fernández, 1993). On the Cíes Islands, the population density of *P. hispanica* is high, reaching 1900–2200 specimens/ha in the most favorable locations (unpubl.).

This archipelago has a Wet Oceanic climatic type (Carballeira et al., 1983), characteristic of coastal areas of the northwest Iberian Peninsula. The mean annual temperature on the islands is 13.7 C, with little within-year temperature oscillation: the mean temperature of the coldest month (January, mean temperature 8.0 C) is only 11.8 C lower than that of the warmest month (July, mean temperature 19.8 C). Annual rainfall: 857 mm/yr (Martínez-Cortizas and Pérez-Alberti, 1999).

Study species.—The Iberian wall lizard, P. hispanica, is a species with a broad distribution throughout the Iberian Peninsula, southern France, and some parts of North Africa (Guillaume, 1997), although recent studies would suggest that the North African populations as well as some in the south of the Iberian Peninsula might belong to different taxa (Harris and Sá-Sousa, 2001). This species mainly inhabits areas belonging to the Mediterranean region. However, populations from northern Portugal and northern Spain (like the one under study in this paper) live in the Euro-Siberian region (Sá-Sousa and Pérez-Mellado, 2002). It is a small (adult snout-vent length 42-65 mm), diurnal, heliothermic, insectivorous lizard of the family Lacertidae that is very variable both in morphology and life-history characteristics (Pérez-Mcllado, 1998). This lizard is mainly a rupicolous species. Nevertheless, on the Cíes Islands, as well as in other places where it is the only representative of the genus Podarcis, it is a ubiquitous and opportunist species, occupying all the available, natural or anthropized biotopes.

Lizards live mainly on rocky cliffs, rocky slopes, stone walls, sides of the roads, and other places with bare ground, rocks, or stones. The activity of these animals peaks during March to October; however, a large number of specimens were still active on sunny winter days.

Data collection.—Data were collected in the course of a study conducted between February 1999 and November 2000 on the Cíes Islands. The study site was visited 1–3 times per month, and on each visit, the number of lizards and the sex of each were recorded. I also recorded details of all reproductive events (i.e., courtships and matings) observed. Whenever possible, lizards were captured by noosing or by hand,

marked individually by toe-clipping and released, noting identity, sex, reproductive condition, snout-vent length (SVL, to nearest 0.1 mm), tail length (including regenerated parts) and mass (to the nearest 0.1 g). All observations were carried out on live animals only. None of the animals was killed to study their internal organs, and all were later released in the study area.

The reproductive condition of live female lizards was evaluated by ventral palpation to detect enlarged ovarian follicles or oviductal eggs. Other reproductive signs (i.e., copulation marks, lateral skin folds, and field observations of courtship and mating behavior) were also noted. In all cases of prompt recapture of females with mating scars but not visibly pregnant, pregnancy was evident at the time of recapture.

Clutch and hatchling characteristics were investigated on the basis of clutches laid by pregnant females captured on the islands in 1999 and 2000. A number of late-pregnant (i.e., highly distended) females were collected and transported to the laboratory. In the laboratory, the females were housed in terraria (100 \times 50 \times 50 cm) with stones and pieces of bark serving as places of retreat and a 3 cm deep substrate of sand. The terraria received light and heat directly from a 100-W light bulb suspended 15 cm above the terraria floor, creating a thermal gradient for 9 h daily (from 10-19 h, approximately). Mealworm larvae (Tenebrio molitor) and other insects collected in the field, as well as water (containing a mixture of vitamins and minerals) were provided ad libitum. During the remaining hours (from 19-10 h, approximately), the gravid females were placed individually into plastic boxes ($10 \times 10 \times 20$ cm), filled to a depth of approximately 15 cm with soil from the study site. In all cases, the eggs were laid in these plastic boxes and not in the terraria. These females were maintained in the laboratory until the eggs were laid. In every clutch laid in laboratory, I recorded the number, size (length and width), and mass (to the nearest 0.001 g) of the eggs. The characteristics of the eggs were, in all cases, determined within 8 h of laying. After laying, each female was measured (± 0.1 mm), weighed, and then released at the capture site. In all cases, each clutch was unequivocally assigned to an individual female, allowing us to calculate the relative clutch mass as the mass of the clutch (immediately after laying) divided by the mass of the mother (excluding clutch mass).

Each clutch was incubated in the same plastic box until hatching. To ensure near-natural conditions of humidity and temperature, the plastic boxes were half-filled with soil from the study site, sealed with an airtight lid and placed by an open, south-facing window. Room temperature fluctuated between 23 and 26 C during the incubation period.

After hatching, I recorded the SVL, mass, and sex of hatchings. Sex was determined by morphological characteristics, such as the number of transverse rows of ventral scales and the dorsal pattern, which differs between male and female P. hispanica. In a sample of 112 adult males and 192 adult females from the study site, males had 24-29 rows of ventral scales and females 28-33 rows (unpubl.). In individuals having 28-29 rows, sex can be determined on the basis of the black dorsal pattern: Males have a reticulated dorsal pattern, whereas females bear well-dcfined longitudinal stripes. For future identification, offspring were marked individually by toeclipping. After all the data were recorded, the hatchlings and their mothers were released at the study site, at the spot where the females were captured.

I have compared the reproductive characteristics of the Cíes island population of *P. hispanica* with data available for other mainland populations of the same species. I calculated the regression equations between each reproductive trait of these populations and mean adult female snout–vent length for populations of *P. hispanica*. The equations were then used to calculate the predicted value of each trait at the average female snout–vent length of the Cíes island population (see Castilla and Bauwens, 2000a).

All statistical analyses were done using the Statview IV statistical package. In the text and tables, mean values are cited \pm SE. When parametric analyses were used, the normality of all data was first confirmed (Kolmogorov-Smirnov test).

RESULTS

Reproductive cycle.—Enlarged follicles were detected by ventral palpation from the beginning of March to July. Ovulation occurred from mid-March to the second half of July because, during this period, I observed females with oviductal eggs. Courting behavior and copulation were observed from early April to early July, in both years of study. The laying period extended from early (1999) or late (2000) April to the second half of July (both years).

Sexual maturity in females.—The smallest reproductive female (collected with oviductal eggs and subsequent oviposition in laboratory) mea-

	Mean	SE	Min	Max	n
Reproductive female SVL (mm)	52.0	0.74	42.2	58.5	34
Reproductive female mass (g)	1.77	0.07	1.17	2.37	34
Clutch size	2.88	0.12	2	4	34
Clutch mass (g)	0.697	0.03	0.401	0.997	34
Relative clutch mass	0.395	0.01	0.263	0.534	34
Egg mass (g)	0.244	0.01	0.191	0.322	92
Egg length (mm)	11.00	0.13	8.20	13.65	92
Egg width (mm)	6.08	0.04	5.30	7.05	92
Hatchling SVL (mm)	23.93	0.21	22.05	26.00	86
Hatchling mass (g)	0.289	0.01	0.213	0.377	86

Table 1. Summary of Statistics for Measurements of Reproductive Females, Eggs and Hatchling Size.

sured 42.2 mm SVL. The SVLs of the next three smallest females caught gravid in the field and oviposited in the laboratory were 42.6 mm, 43.9 mm, and 44.0 mm. Thus, females attained sexual maturity at a minimum SVL of about 42–44 mm. Three females marked at hatching in July 1999 were recaptured as breeding adults 11–12 months later, in June and July 2000, confirming that maturation is attained at one year of age.

Clutch and hatchling characteristics.—Neither the reproductive characteristics or female snoutvent length (SVL) and female mass varied significantly among the islands (San Martiño and Monteagudo-Faro islands, Mann-Whitney test, P > 0.05 in all cases). In the following sections, I thus consider data for the three islands together. Similarly, none of the characteristics listed varied significantly between the two years of study (Mann-Whitney test, P > 0.05 in all cases). Therefore, the data from both years were considered jointly. The characteristics of the reproductive females, their clutches and the juveniles subsequently hatched are summarized in Table 1.

Clutch size, clutch mass, and egg mass increased significantly with the mother's SVL;

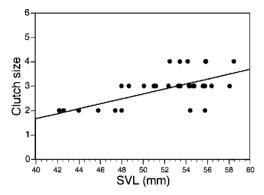


Fig. 1. Relationships between mother's hody size (snout-vent length, SVL) and clutch size.

clutch size: r=0.64, $F_{1,32}=21.64$, P<0.0001; clutch mass: r=0.84, $F_{1,32}=72.79$, P<0.0001; egg mass: r=0.48, $F_{1,32}=9.18$, P=0.005. (Figs. 1–2). The relative clutch mass was not significantly related to the mother's SVL (r=0.25, $F_{1,32}=2.08$, P=0.16).

The mean hatchling mass in each clutch and the mean hatchling SVL in each clutch increased significantly with mean egg mass (mean hatchling mass: r=0.81, $F_{1.26}=48.86$; mean hatchling SVL: r=0.84, $F_{1.26}=57.71$, P<0.0001 in both cases). Also, the mean hatchling SVL in each clutch increased significantly with the mother's SVL (r=0.45, $F_{1.26}=6.36$, P=0.018), and the mean hatchling mass in each clutch increased significantly with the mother's mass (r=0.58, $F_{1.26}=12.59$, P=0.002). Hence, larger and heavier females laid larger and heavier eggs, and larger eggs produced larger and heavier hatchlings.

The relationships between residuals from the regression of log (clutch size) on log (mother's SVL) and residuals from the regression of log (mean egg mass) on log (mother's SVL) were

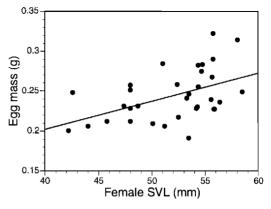


Fig. 2. Relationships between mother's hody size (snout-vent length, SVL) and average single-egg mass in each clutch.

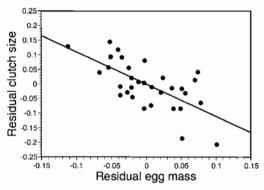


Fig. 3. Relationships between residual deviations of clutch size (residual values of the regression of log clutch size on log mother's SVL) and residual deviations of average single-egg mass in these clutches (residual values of the regression of log egg mass on log mother's SVL).

again significant (r = -0.67, $F_{1.32} = 25.61$, P < 0.0001). Considering clutches laid by females of about the same size, the mean mass of the eggs in a clutch is thus negatively correlated with clutch size (Fig. 3).

Clutch frequency.—Mark-recapture records for a number of females caught during the breeding season of 1999 and 2000 provided information on clutch frequency. The larger females (SVL > 55 mm) initiated reproductive activities early in

the season (observed with enlarged follicles or oviductal eggs from March or early April) and produced two to three clutches annually, whereas the smaller individuals (SVI. <50 mm) laid only a single clutch and initiated reproduction in June or July.

Characteristics (SVL and mass) of the females that produced only a single clutch per year and females that produced 2–3 clutches in the same season their clutches and the juveniles subsequently hatched are summarized in Table 2. These two size/age classes of females differ significantly in all the reproductive characteristics, except in relative clutch mass and mean juvenile mass.

Hatch success and hatchling sex ratio.—Of the 97 eggs laid in the laboratory, 92 (94.8%) were viable at oviposition, and of these, 86 hatched normally, indicating that hatch success, estimated considering all clutches together, was very high (93.5%).

The sex ratio of clutches hatched in the laboratory was 1:0.76 (49 males to 37 females). This ratio does not differ significantly from one-to-one ($\chi^2 = 1.67$, df = 1, P = 0.20). None of the hatchlings hatched in the laboratory was visibly malformed.

DISCUSSION

Several studies have reported on the reproductive characteristics of different Iberian pop-

Table 2. Summary of Statistics for Reproductive Females, Clutches, and Hatchling Characteristics for Individuals that Laid Only One Clutch a Year and Individuals that Oviposited Several. (2 or 3) Clutches in One Reproductive Season. Shown are the mean \pm 1 SE and the sample size (n). U indicates the value of the Mann-Whitney test and P the significant value between monoestrous and polyestrous females in all characteristics.

	Females that laid 1 clutch per season		Females that laid 2–3 clutches per season		C	
•	Mean ± 1 SF. (range)	n	Mean ± 1 SE (range)	n	- Comp	parisons P
Reproductive female SVL (mm)	46.99 ± 0.81	12	54.98 ± 0.36	20	240	0.0001
•	(42.2-51.1)		(52.4-58.5)			
Reproductive female mass (g)	1.42 ± 0.05	12	1.98 ± 0.07	20	227	0.0001
.,	(1.168-1.727)		(1.459 - 2.733)			
Clutch size	2.33 ± 0.14	12	3.20 ± 0.14	20	200	0.0007
	(2-3)		(2-4)			
Clutch mass (g)	0.540 ± 0.04	12	0.796 ± 0.02	20	221	0.0001
-	(0.401 - 0.853)		(0.565 - 0.997)			
Relative clutch mass	0.376 ± 0.02	12	0.407 ± 0.02	20	158.5	0.134
	(0.303 - 0.514)		(0.263 - 0.534)			
Egg mass (g)	0.231 ± 0.01	12	0.254 ± 0.01	20	178.5	0.049
	(0.200 - 0.284)		(0.191 - 0.322)			
Hatchling SVL (mm)	23.26 ± 0.33	12	24.21 ± 0.24	20	114.5	0.041
	(22.05 - 24.85)		(22.37 - 26.00)			
Hatchling mass (g)	0.271 ± 0.01	12	0.296 ± 0.01	20	91.5	0.410
_	(0.217 - 0.305)		(0.213 - 0.377)			

Table 3. Reproductive Characteristics of Different Populations of *Podarcis hispanica* and Other Insular *Podarcis* Species. The observed value for *Podarcis hispanica* from the Cies Islands is compared to the predicted value obtained from regression equations.

Location	Mean SVL (mm)	SVL at maturity (mm)	Clutch size	Egg mass (g)	Clutch mass (g)	Source
Cíes Islands						This study
Observed	52.0	42.2	2.88	0.244	0.697	
Predicted		43.8	2.69	0.281	0.753	
Other <i>Podarcis hispanica</i> p	opulation:	s				
Asturias and Cantabria	47.6		2.2			Braña (1996)
Asturias	49.6	39.4	2.1	0.27	0.58	Braña in Castilla and Bauwens (2000a)
Sierra de Gredos	50.4	43.9	2.6			Gil (1992)
Sistema Central	50.6	44.0	2.5			Pérez-Mellado (1982)
Galicia (A Coruña)	50.7	43.0	3.1	0.24	0.73	Galán, unpubl.
Asturias	51.8		2.3	0.30		Braña et al. (1991)
Madrid	56.7	46.3	3.0	0.33	1.01	Castilla and Bauwens (2000a)
Sierra de Guadarrama	57.1	49.4	3.6			García-Fernández (1990)
Salamanca	61.3	50.0	3.6	0.34	1.22	Castilla and Bauwens (2000a)
San Sebastián	61.6		4.0	0.33	1.32	Braña et al. (1991)
Other insular <i>Podarcis</i> spe	cies					
Podarcis atrata	63.1	51.0	2.8	0.37	1.14	Castilla and Bauwens (2000a)
Podarcis lilfordi	61.9	50.0	2.5	0.63	1.50	Castilla and Bauwens (2000b)
Podarcis milensis	50.4	42.0	1.73			Adamopoulou and Valakos (2000)

ulations of P. hispanica. Castilla and Bauwens (2000a) have compiled this information and present unpublished data, as well as data on the insular population of *P. atrata*, which has long been considered a subspecies of P. hispanica. However, a recent study using molecular markers warranted elevating it to species status (Castilla et al., 1998). On comparing these data with those collected in this study, I observed that the reproductive characteristics of the population of P. hispanica on the Cies Islands did not differ from the characteristics of other mainland populations of the same species having a similar body size. Female P. hispanica from the Cíes exhibited a body length roughly midway between that of the other populations of the same species previously studied (Table 3). Despite their insular condition, the mean body length of these animals was markedly shorter than in other continental populations such as in the Sierra de Guadarrama or Salamanca. The clutch size was slightly larger and clutch mass, single egg mass, and SVL of females at maturity slightly smaller but within the range of values expected for a hypothetical population of P. hispanica with the mean adult female SVL being the same as that observed in Cíes population (Table 3).

Although there have been no comparative phylogenetic studies undertaken as yet focusing

on the differences in reproductive characteristics between insular and mainland species of lacertid lizards that would point to the consistency of certain evolutionary patterns, available evidence shows that the production of clutches comprising relatively few, but large eggs is a characteristic found in some island species of *Podarcis* (Castilla and Bauwens, 2000a,b; unpubl.), as well as in other lacertid lizards (Rodríguez-Domínguez and Molina-Borja, 1998; Galán and Vicente, 2003; unpubl.). This difference, nonetheless, was not observed between the insular population of *P. hispanica* studied and the mainland populations of the same species.

Several hypotheses may be proposed to explain the lack of major differences in reproductive traits between the Cíes and the mainland populations. The first has to do with the short length of time that this population has been isolated, dating back only approximately 8000–9000 yr, when the Cíes broke off from the mainland owing to changes in sea level (Dias et al., 2000). This period of isolation may have been too short to allow for a detectable evolutionary divergence in reproductive characteristics. In the insular populations of *Podarcis* where a divergence is manifest, the isolation occurred as far back as a million years, in the case of *P. atrata* on the Columbretes islands, or several million

years in the case of *P. lilfordi* on the Balearic Islands (Castilla and Bauwens, 2000a,b).

The second hypothesis is that the selection gradient for reproductive traits on the Cíes Islands may have remained similar to that on the mainland. Indeed, when conditions on islands are similar to those on the mainland, then there will be no divergent selection pressure and hence no reason to expect a (rapid) evolutionary change.

The third hypothesis is based on the notion that egg size is probably constrained by the volume of the oviducts, the body cavity, and the pelvic width of this species, which is small in size with a flat shaped body. The mainland populations of P. hispanica, which have a body size similar to that of the Cíes population, already sliow a very small clutch size, around two or three eggs on average, related to these morphological traits (Braña, 1983; Galán, 1986). Therefore, the egg size is restricted by the width of the pelvic belt in the females of these populations. which have a small body size. Another constraint is imposed by the limited volume of the abdominal cavity in this flat-bodied, crevicedwelling species, which prevents these animals from laying larger sized eggs. This holds true even in an insular population where a large hatchling body size would warrant preferential selection.

However, these putative limitations on egg size cannot explain the absence of decline in clutch size without a concomitant increase in egg size. The reduction in clutch size could then be compensated by an increase in the number of clutches produced in a reproductive scason. This seems to have occurred in P. milensis, an island species that is similar in body size (average female SVL: 50.4 mm) but that has a smaller clutch size (average: 1.7 eggs per clutch) than P. hispanica. About 33-44% of females P. milensis lay clutches composed of only a single egg (Adamopoulou and Valakos, 2000). It is interesting to note that in my study population of P. hispanica I have never observed a clutch made up of just one egg.

Such small clutch sizes in *P. milensis* may be related to the fact that this species undergoes an unusually long laying period for a temperate climate—seven months—between January and August (thanks to the Mediterranean climate, which makes it possible for females to start laying very early, in the middle of winter). During this period, females may lay eggs several times (Adamopoulou and Valakos, 2000), thus distributing the reproductive effort over numerous clutches consisting of only one or two eggs. *Podarcis hispanica* of the Cíes Islands, however, has

a reproductive period lasting far less than four months (because this species lives in an Atlantic climate where the winters are colder than in the Mediterranean and the laying period does not begin until spring). Hence, they must concentrate their reproductive investment on a smaller number of clutches (between one and three), each composed of several eggs. In keeping with this idea, Sinervo and Licht (1991) have conducted experiments that demonstrate the anatomical causes and energy distribution responsible for the scarcity of saurian species having clutches consisting of a single egg.

My results indicate that female P. hispanica from the Cícs Islands may produce multiple clutches (two or three) per year, as do some other species of the genus Podarcis (e.g., Galán, 1997; Castilla and Bauwens, 2000a,b). The number of clutches laid per year differs among individual females, depending on their body size. Large females produce two or three clutches annually, and the smallest mature individuals lay only a single clutch, as in other lizard species (e.g., Bauwens, 1999). It is important to highlight the fact that the differences between small sized females (young animals) and the larger ones (old animals) do not refer only to the number of clutches laid annually but also apply to other reproductive traits, including the number of offspring and their size. Variation in clutch size was rather restricted in this population, ranging between two and four eggs; nevertheless, I found a significant relationship between the existing variation in clutch size and female size (SVL). This increase in egg number with female size is a general phenomenon in lizards with variable clutch size, including lacertid lizards (e.g., Barbault and Mou, 1988; Braña, 1996; Galán, 1997). However, this relationship is absent in some populations of P. hispanica from Asturias and Cantabria, in Northern Spain (Braña et al., 1991; Braña, 1996).

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LITERATURE CITED

- ADAMOPOULOU, C., AND E. D. VALAKOS. 2000. Small clutch size in a Mediterranean endemic lacertid (*Podarcis milensis*). Copcia 2000:610–614.
- 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. 1999. Life-history variations in lacertid lizards. Nat. Croat. 8:239–252.
- BRAÑA, F. 1983. La reproducción de los saurios de Asturias (Reptilia; Squamata): ciclos gonadales, fecundidad y modalidades reproductoras. Rev. Biol. Univ. Ovicdo 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.
- Carballeira, A., C. Devesa, R. Retuerto, F. San-Tillán, and F. Ugieda. 1983. Bioclimatología de Galicia. Ed. Fundación Pedro Barrié de la Maza, La Coruña, Spain.
- CARRETERO, M. A., G. LLORENTE, X. SANTOS, AND A. MONTORI. 1995. Características reproductoras de una población introducida de *Podarcis pityusensis*. Rev. Esp. Herpetol. 9:93–102.
- Case, T. J. 1983. Niche overlap and the assembly of island lizard communities. Oikos 41:427–433.
- Castilla, A. M. 1996. Temperature selection for egg incubation by the lizard *Podarcis hispanica atrata*. Herpetol. J. 6:133–136.
- ______, AND D. BAUWENS. 2000a. Reproductive characteristics of the lacertid lizard *Podarcis atrata*. Copeia 2000:748–756.
- ——, AND ——. 2000b. Reproductive characteristics of the island lacertid lizard *Podarcis lilfordi*. J. Herpetol. 34:390–396.
- ——, 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 Columbetes Islands merits specific distinction. Copeia 1998:1037–1040.
- DIAS, J. M. A., T. BOSKI, A. RODRIGUES, AND F. MAGAL-HAES. 2000. Coast line evolution in Portugal since the Last Glacial Maximum until present—a synthesis. Mar. Geol. 170:177–186.

- GALÁN, P. 1986. Morfología y distribución del género Podarcis Wagler, 1830 (Sauria, Lacertidae) en el noroeste de la Península Ibérica. Rev. Esp. Herpetol. 1:85–142.
- ——. 1997. Reproductive ecology of the lacertid lizard *Podarcis bocagei*. Ecography 20:197–209.
- ——, AND G. FERNÁNDEZ, 1993. Anfibios e réptiles de Galicia. Edicións Xerais, Vigo, Spain.
- ——, AND I. VICENTE. 2003. Reproductive characteristics of the insular lacertid *Teira dugesii*. Herpetol. J. In Press.
- GARCÍA-FERNÁNDEZ, J. 1990. Dieta y reproducción de Podarcis hispanica y Podarcis muralis en la Sierra de Guadarrama. Unpubl. master's thesis. Univ. of Salamanca, Salamanca, Spain.
- GIL, M. 1992. Estudio de la comunidad de saurios de la vertiente meridional de la Sierra de Gredos. Unpubl. Ph.D. diss. Univ. of Salamanca, Salamanca, Spain.
- GRANT, B. R., AND P. R. GRANT. 1989. Evolutionary dynamics of a natural population: the large cactus finch of the Galápagos. Univ. of Chicago Press, Chicago.
- GRANT, P. R. 1998. Patterns on islands and microevolution, p. 1–17. *In*: Evolution on islands. P. R. Grant (ed.). Oxford Univ. Press, Oxford.
- GUILIAUME, C. P. 1997. Podarcis hispanica (Steindachner, 1870), p. 278–279. In: Atlas of Amphibians and Reptiles in Europe. J.-P. Gasc, A. Cabela, J. Crnobrnja-Isailovic, D. Dolmen, K. Grossenhachner, P. Haffiner, J. Lescure, H. Martens, J. P. Martínez-Rica, H. Maurin, M. E. Oliveira, T. S. Sofiandou, M. Veith, and A. Zuiderwijk (eds.). Societas Europea Herpetologica and Muséum National d'Histoire Naturelle (IEGB/SPN), Paris.
- HARRIS, D. J., AND P. SÁ-SOUSA. 2001. Species distinction and relationships of the Western Iberian *Podarcis* lizards (Reptilia, Lacertidae) based on morphology and mitochondrial DNA sequences. Herpetol. J. 11:129–136.
- KRAMER, G. 1946. Veranderungen von nachkommenziffer und nachtkommengrosse sowie der altersverteilung von inseleidechsen. Z. Nat. forsch. 1:700– 710.
- MARTÍNEZ-CORTIZAS, A., AND A. PÉREZ-ALBERTI. 1999. Atlas climático de Galicia. Consellería de Medio Ambiente, Xunta de Galicia, Santiago de Compostela, Spain.
- 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.
- . 1998. Podarcis hispanica (Steindachner, 1870), p. 258–272. In: Fauna Ibérica. Vol. 10. Reptiles. A. Salvador (coord.) and M. A. Ramos, J. A. Tercedor, X. Bellés, J. Gosálbez, A. Guerra, E. M. Mayol, F. Martin, J. Sevrano, and J. Templado (eds.). Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain.
- RODRÍGUEZ-DOMÍNGUEZ, M. A. AND M. MOLINA-BORJA. 1998. Reproduction of the endangered Hierro giant lizard *Gallotia simonyi machadoi*. J. Herpetol. 32: 498–504.
- SÁ-SOUSA, P., AND V. PÉREZ-MELLADO. 2002. Podarcis

hispanica (Steindachner, 1870). Lagartija ibérica, p. 244–245. *In*: Atlas y libro rojo de los anfibios y reptiles de España. J. M. Pleguezuelos, R. Márquez, and M. Lizana (eds.). Dirección General de Conservación de la Naturaleza-A.H.E., Madrid, Spain.

Sinervo, B., and P. Licht. 1991. Proximate constraints on the evolution of egg size, number, and total clutch mass in lizards. Science 252:1300–1302.

VICENTE, L. A. 1989. Sobre a história natural dos répteis da ilha Berlenga. A sindrome de insularidade. Unpubl. Ph.D. diss., Univ. of Lisbon, Lisbon, Portugal.

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