Amphibia-Reptilia 10 (1989): 201-213, E.J. Brill, Leiden

Observations on the natural history of *Lacerta lepida* in Cádiz Province, Spain

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Abstract. Cádiz Province, Spain, is the southernmost extent of the range of *L. lepida*. Within this area, *L. lepida* demonstrates no distinct preference for any habitat and inhabits man-made and natural shelters with equal frequency. *L. lepida* is diurnal and active at the surface at ambient temperatures between 15.6°C and 42°C from February through November. Males are 4% to 8% heavier than females of equivalent body length. The rate of parasitism from nematodes is low (6%).

The Cádiz Province population has the most diverse diet of any population studied to date. The taxonomic composition of the diet of males and females is identical, and consists mostly of invertebrate prey. Mean prey size and prey diversity are not correlated with lizard body size. *Lacerta lepida* is cannibalistic.

Spermatogenesis and follicular development occur from April through July, egg laying occurs between early June and early July, and clutch size may vary from 4 to 18. *Lacerta lepida* reproduces only once annually.

Introduction

During the course of zoogeographical, morphological, and genetic analyses of the amphibians and reptiles of southern Spain, we have observed and studied aspects of the natural history of *Lacerta lepida* in some detail. Comparative morphological and genetic analyses of *L. lepida* and *L. pater* have appeared elsewhere (Busack, 1987). The following report details our observations of the natural history of *Lacerta lepida* in Cádiz Province, Spain.

Material and methods

Between March, 1969, and February, 1972, observations on the ecology of *L. lepida* were recorded in conjunction with a biogeographical survey of the amphibians and reptiles of Cádiz Province, Spain (see Busack, 1977, for methodology). These observations were augmented by data and specimens obtained from March through June, 1982, and from March through April, 1983. Each specimen collected was preserved

immediately in 10% formalin and transferred to 70% ethyl alcohol for permanent storage.

Specimens examined

Lacerta lepida—Carnegie Museum 50948, 51043-51044, 51082, 51085, 51103-51104, 51918, 51946, 52021, 52180-52181, 52621, 53060, 53133, 53136-53138, 53176-53177, 53185, 53201-53212, 53218, 53224, 53298, 53303 (4 eggs), 53316, 53360, 53365-53366, 53370, 53418, 53905, 53917-53918, 53919, 54214, 54235, 54268, 54570, 54595, 54689, 54797-54799, 54865, 54870, 54877, 54879, 55332, 55349, 55439-55440, 55449, 55469, 55493, 55497, and 55669-55673; Museum of Vertebrate Zoology, University of California, Berkeley 186055-186071; National Museum of Natural History, Washington 195464; SDB field series (housed at the Museo Nacional de Ciencias Naturales, Madrid, Spain) 931, 955-960, 972-974, 994-995, 1041-1046, 1061-1062, 1537, 1572, 1660, and 1672.

Abbreviata abbreviata (Nematoda: Physalopteridae)—Muséum National d'Histoire Naturelle, Paris, Laboratoire des Vers, 83BC-88BC.

Habitat utilization

Collections and observations provide precise locality data for *L. lepida* and other lizards within Cádiz Province (Busack, 1977, and unpublished field notes). Because these data contain several replications of a single locality, and we were interested in determining habitat generality or specificity, only the first appearance at a specific locality was included in calculations. A single occurrence in any habitat type is sufficient to document the presence of any species in that habitat type.

The Instituto Nacional de Investigaciones Agronomicas (INIA, 1971) provides a 1:200,000 scale map of Cádiz Province, Spain, on which 13 categories of cultivated and unimproved (salt flats, sclerophyllous shrub, etc.) land are identified. We were able to assign all unique sites for *L. lepida* and other lizards to a specific category of land use (= habitat type) on this INIA map. Each specimen occurring at a unique locality for its species was recorded, and the total number of occurrences of each species in each of the 13 habitat categories was calculated. Spearman's rank correlation (r_S; Zar, 1974) was used to assess whether *L. lepida* utilized habitat types in proportion to the frequency of occurrence of those types within Cádiz Province, Spain.

An information theoretic index (Brillouin's measure H'; see Poole, 1974; Busack, 1980) based on the number of occurrences of each species in each habitat type enabled us to compute values for diversity of habitat-use; natural logarithms were used in these computations. We evaluated inter-specific overlap in habitat use with Pianka's (1974) symmetric overlap measure.

Thermal Environment

Ambient temperatures for general observations were recorded on a Weksler bi-metal thermometer, shaded from the sun, at a distance of approximately one meter from the surface of the ground. Lizard cloacal temperatures, and corresponding ambient temperatures, were recorded with a Schultheis rapid-recording thermometer. Cloacal

temperature was ascertained by cloacal probe within 1 minute of capture; ambient temperature was taken with the same thermometer 1 cm above the surface upon which the lizard was sitting at the time of capture. All thermometers were calibrated.

Diet

Taxonomic composition

Prey items were removed from the stomachs of 39 male and 45 female *L. lepida*, placed in a transparent petri dish, and identified to order. Intact prey items were measured. The total length of each invertebrate was approximated by comparison with 0.5 mm graduations of a translucent ruler placed under the dish. The only vertebrate prey item encountered was a young *L. lepida*; the snout-vent length (SVL $\approx$ 46 mm) of the ingested *L. lepida* was determined by comparing measurements of undigested remains with those of intact Cádiz Province specimens of approximately the same proportions.

Quantitative procedures

Numbers of prey items per individual stomach, and numbers of empty stomachs, were recorded and arranged by sex. Mean prey size (MPS), as used below, is the grand mean obtained by multiplying the length of an individual prey item by the number of items of that length, summing these values over all prey lengths represented, and dividing by the total number of measurable items in the stomach.

We evaluated correlation between SVL and the total length of the largest prey item in the stomach, MPS, and diet diversity, by sex with Spearman's Rank Correlation Coefficient. Trophic diversity and evenness of prey-type representation per individual were computed with Brillouin's diversity index (natural logarithms; Pielou, 1969; Busack, 1980) and also arranged by sex. Comparative feeding data (tables 1 and 2) from populations outside of Cádiz Province (fig. 1), were obtained from Valverde (1967), Mellado et al. (1975), Cheylan (in Bischoff et al., 1984), Perez Mellado (1981:182), and Peters (1962).

Weight-length relationship

The SVL of freshly killed specimens was determined to the nearest mm with a metal ruler. Pesola field balances, calibrated in the laboratory prior to field use and accurate to 0.5 g, were used to estimate body mass.

Allometric weight-length difference between sexes was assessed by Analysis of Covariance. Weight and length data were transformed prior to this analysis; weight was entered as the cube root of the actual weight, SVL was entered as the natural logarithm (ln) of actual SVL.

The relationship between weight and length within each sex was assessed by linear

Figure 1. Localities in France, Spain, and Portugal at which the diet of *Lacerta lepida* has been studied. A = Cádiz Province, Spain; B = Almería, Spain; C = Sierra Morena; D = Sierra de Cazorla; E = Sierra de Béjar, Sierra de Francia, Sierra de Gata, and Sierra de Estrella; F = Valladolid, Spain; G = Bouches-du-Rhône, Vaucluse, Hérault, Aude, and Pyrénées-Orientales Departements, France.

regression. The mm equivalent of SVL was entered as the independent variable and the cube root equivalent of weight was entered as the dependent variable.

Statistical probabilities given are those for committing a type I error in a two-tailed test.

Reproductive cycles

Peters (1962: table 3) determined that males ≥ 133 mm snout-vent length (SVL) and females ≥ 124 mm SVL were mature; we examined only males and females of comparable size to assess seasonal changes in reproductive condition. Testes were removed from 18 mature males collected between April and November and prepared for microscopic analysis following procedures described by Berg (1953). Testicular sections mounted on slides were examined microscopically for the cellular stages of spermatogenesis and later deposited with Carnegie Museum of Natural History. Ovarian follicles were measured *in situ* with an ocular micrometer in 22 adult females collected between March and November. The lengths of oviductal eggs were measured *in situ* with dial calipers accurate to 0.1 mm.

Results and Discussion

Habitat Utilization

Lacerta lepida utilizes the highest diversity of habitats among the ten lizard species found within Cádiz Province (table 3). When the 184 unique sites at which *L. lepida*

Table 1. Taxonomic composition of the diet of *L. lepida* within Cádiz Province, Spain, and throughout its range. Localities (A-G) are identified in figure 1, figures are numerical proportions, diet diversity and evenness are measured with Brillouin's index.

	within Cádiz		localities						
prey categories	*males*	*females*	*A*	*B*	*C*	*D*	*E*	*F*	*G*
Gastropoda	0.096	0.052	0.070	0.027	0.011	0.079	—	0.027	0.071
Arachnida									
Araneae	0.006	0.019	0.014	0.005	0.013	—	0.023	—	0.016
Phalangida	—	—	—	—	0.005	—	0.004	—	0.005
Scorpionida	—	—	—	—	0.001	—	—	—	0.005
Crustacea									
Isopoda	0.128	0.207	0.173	0.044	0.005	—	—	—	0.022
Chilopoda	0.032	0.009	0.019	0.005	0.004	0.011	—	—	—
Diplopoda	0.006	—	0.003	—	—	—	0.005	—	0.011
Insecta									
Coleoptera	0.423	0.352	0.382	0.699	0.684	0.438	0.560	0.703	0.538
Dermoptera	—	0.014	0.008	—	0.003	—	—	—	0.005
Dictyoptera	0.013	0.009	0.011	—	—	—	—	—	0.011
Diptera	0.006	0.028	0.019	0.003	0.010	0.011	0.023	0.068	0.016
Hemiptera	—	0.019	0.011	—	0.006	0.056	0.007	0.122	0.038
Hymenoptera	0.090	0.080	0.084	0.107	0.042	0.101	0.249	—	0.082
Lepidoptera									
(larvae)	0.096	0.066	0.079	—	0.050	—	0.057	—	0.033
(adults)	—	—	—	—	0.001	—	0.007	—	—
Neuroptera	0.006	—	0.003	—	—	—	—	—	—
Orthoptera	0.090	0.141	0.119	0.041	0.018	0.022	0.041	0.014	0.132
unidentified									
larvae	0.006	—	0.003	0.068	0.094	0.281	0.021	0.068	0.011
Aves									
Alaudidae	—	—	—	—	—	—	0.002	—	—
Reptilia									
L. lepida	—	0.005	0.003	—	—	—	—	—	—
unidentified									
vertebrate	—	—	—	—	0.003	—	—	—	—
total diet items	156	213	369	365	2919[a]	89	559	74	182[b]
specimens									
examined	39	45	84	29	158	16	33	6	31
$\bar{x}$ prey items/									
individual	4.0	4.7	4.4	12.6	—	5.6	16.9	12.3	—
diet:									
diversity	1.72	1.82	1.83	1.07	—	1.37	1.31	0.92	1.57
evenness	0.71	0.75	0.70	0.50	—	0.71	0.54	0.56	0.61

[a] Total includes seeds and unidentified items; proportional contributions for identified prey were transcribed directly from Mellado et al., 1975.

[b] Constructed from data provided by Cheylan (in Bischoff et al., 1984) and Peters (1962).

was observed were partitioned into categories of habitat type, and the proportion of sites within each habitat type was compared to the proportion which each habitat type contributes to Cádiz Province (table 4), the association was significant ($r_S = 0.88$, $p < 0.005$). *Lacerta lepida* inhabits each category of habitat type within Cádiz Province

Table 2. Diet similarity among populations of *L. lepida*. Localities A-G are identified in figure 1.

	localities						
	A	B	C	D	E	F	G
A	—	0.89	0.86	0.75	0.86	0.84	0.93
B		—	0.99	0.88	0.96	0.97	0.97
C			—	0.89	0.93	0.98	0.96
D				—	0.83	0.87	0.84
E					—	0.89	0.94
F						—	0.95

Table 3. Habitat use and diversity among the lizard species of Cádiz Province, Spain.

Species	number of unique localities	diversity (Brillouin's H')
L. lepida	184	1.54
Acanthodactylus erythrurus	14	0.67
Podarcis hispanica	149	1.21
Psammodromus algirus	88	1.38
P. hispanicus	10	0.94
Chalcides chalcides	15	1.16
C. bedriagai	1	0.00
Chamaeleo chamaeleon	6	0.68
Hemidactylus turcicus	6	0.87
Tarentola mauritanica	116	1.03

Table 4. Rank order comparison between proportion of habitat type within Cádiz Province, Spain, and proportion of habitat use by *L. lepida*.

habitat type	proportion of province	proportion of use by *L. lepida*
sclerophyllous shrub	22.40	39.6
unirrigated crops	27.30	22.2
grassland	7.30	15.2
pasture	15.00	12.5
open oak woodland	4.80	5.4
riparian pasture	3.20	1.6
agriculturally unproductive	15.84	1.6
irrigated crops	1.50	1.0
citrus fruits	0.10	0.5
irrigated vineyards	1.92	0.0
vineyards and truck farms	0.58	0.0
rice	0.04	0.0
orchards	0.01	0.0

Spearman's Rank Value: 0.88, $p < 0.005$.

in direct proportion to that category's abundance in the Province; no overt preference for any habitat type was detected.

Among the lizard species inhabiting Cádiz Province, *L. lepida* appears the most opportunistic in terms of habitat utilization. While *L. lepida* finds shelter in naturally occurring piles of rock and beneath fallen trees, it as frequently finds shelter in retaining walls, bridge abutments and culverts. Fully 50% of our recorded occurrences place *L. lepida* in man-made structures.

Activity periods

Annual

Lacerta lepida is active from February to November in Cádiz Province (Busack and Jaksić, 1982: fig. 3). May is the month of maximum activity (83 of 233 observations [36%] were recorded during May), followed by June (15%), April (10%) and July (10%), and October (9%). August and September, generally the hottest and driest months, account for only 7% and 6% of the total, respectively. March (3%), November (2%), and February (2%) account for the remaining observations.

Diel

Figure 2 provides a summary of daily surface activity for the Cádiz Province population throughout the year. The briefest period of activity recorded (15 minutes) was during February, the longest period during which at least one lizard was active at the surface (9.8 h) occurred during May. Bimodal activity, characterized by an absence of specimens at the surface during mid-day, begins in June and continues through September.

Lacerta lepida is strictly a diurnal lizard; the earliest recorded time of surface activity was 0826 h (during July) and the latest was 1949 h (during May). Thirty-eight percent of all observations of activity time are concentrated between 1000 h and 1300 h, and 37% were between 1500 h and 1900 h.

Thermal environment

Adult *Lacerta lepida* are active at the surface when ambient temperatures are between 15.6°C and 42°C. Adults that appeared to be absorbing heat through direct exposure to the sun were frequently observed at ambient temperatures between 15.6°C and 28°C. Active adults, those crossing provincial roadways or otherwise moving about the surface, were noted at ambient temperatures as high as 42°C. One adult was observed partially submerged in the water of a permanent stream when the ambient air temperature was 34.4°C.

Sub-adults (specimens displaying juvenile coloration) appear more tolerant of cold,

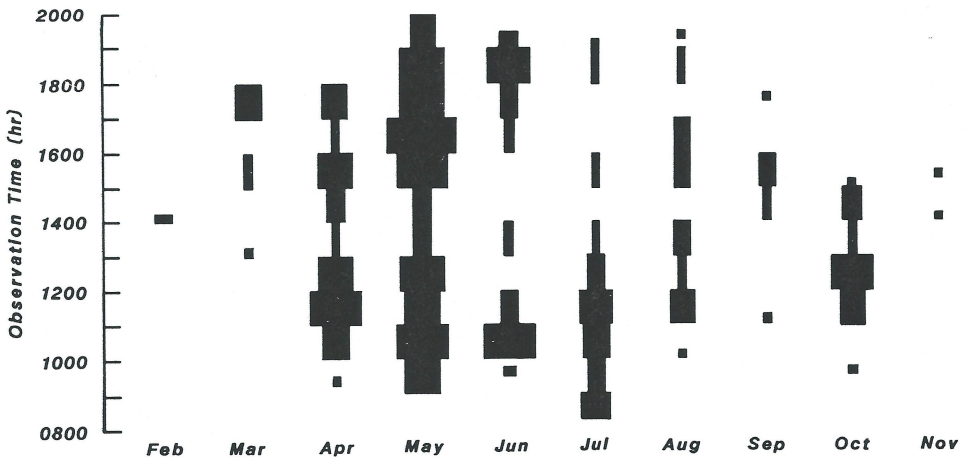

Figure 2. Seasonal and diurnal activity of *Lacerta lepida* (n = 155). Width of bar indicates sample size; narrowest bar (1300 hrs, March, et al.) indicates one observation, widest bar (1600-1700 hrs, May) indicates eight observations.

and less tolerant of heat, than adults. Sub-adult lizards were active at ambient temperatures between 11.1°C and 30°C.

Seven cloacal temperatures of adults (fig. 3) ranged between 21.2°C and 34.5°C ($\bar{x}$ = 30.4°C) while ambient temperatures were between 18°C and 25°C ($\bar{x}$ = 22.7°C). The mean difference between body and ambient temperature was 7.7°C (range 3.2-12°C) in this small sample.

Diet

Taxonomic composition

The taxonomic composition of the diet of male and female *L. lepida* within Cádiz Province, Spain, is virtually identical (Pianka's overlap = 0.96). Insects are numerically the most important prey; coleopterans, orthopterans, hymenopterans, and lepidopteran larvae form 66% of the diet. Other major contributors are isopods (17%) and snails (7%; table 1). Berries and seeds are occasionally ingested (4 females and 3 males contained small amounts of these materials), but these foods do not contribute significantly to the diet. The remains of a juvenile *L. lepida* in the stomach of one adult female specimen indicates that cannibalism does occur.

The diet of *L. lepida* has now been studied in seven populations from throughout its range (fig. 1, table 1). Populations with the most diverse diets were those inhabiting Cádiz Province (fig. 1A), Spain, southeast France (fig 1G), Jaén Province (fig. 1D), Spain, and the Sierras de Béjar, de Francia, de Gata, and de Estrella of Spain and

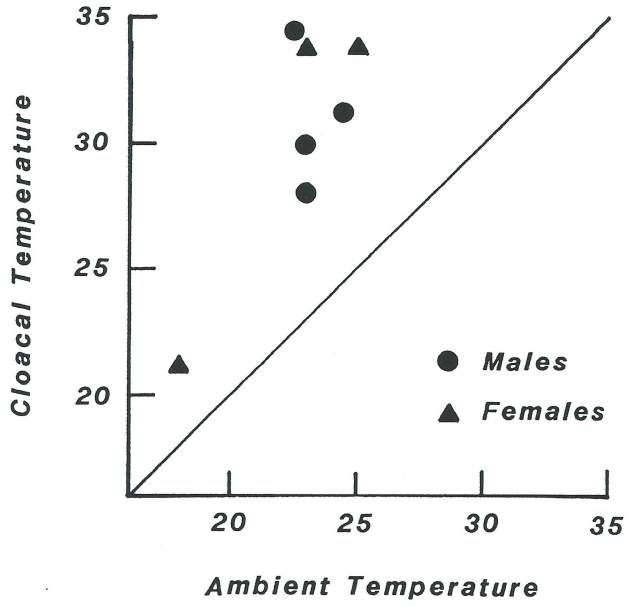

Figure 3. Cloacal vs ambient temperature in 7 *Lacerta lepida*.

Portugal (fig. 1E); lowest diet diversities were found in populations inhabiting areas of Almería (fig. 1B) and Vallodolid (fig. 1F) Provinces, Spain (table 1).

Diet similarity among populations is high (table 2). The diets of populations from Jaén and Cádiz Provinces, Spain, are least similar (0.75), while diets of populations from Almería and Huelva Provinces, Spain, are most similar (0.99).

Lacerta lepida is an opportunistic predator that is basically an insectivore. Coleopterans, the most commonly reported food item, comprise between 38% and 70% of the diet at each locality studied. Except for the Cádiz population, where isopods comprise 17% of the diet by number of items, only insect orders reach or exceed a diet proportion of 10%. Other food items, including bird eggs (Valverde, 1967; de Juana and de Juana, 1982), small vertebrates (table 1), and plant materials, are only occasionally consumed.

Quantitative description

There is no significant relationship between mean prey size (MPS; $n = 29$, $r_s = 0.32$, $p > 0.05$ for males, $n = 33$, $r_s = -0.07$, $p >> 0.05$ for females) or prey diversity ($n = 20$, $r_s = 0.39$, $p > 0.05$ for males; $n = 26$, $r_s = 0.21$, $p >> 0.05$ for females) and lizard size (SVL). The largest prey a male specimen takes is directly related to his size ($n = 30$, $r_s = 0.40$, $p < 0.05$) however, while the largest prey a female specimen takes is not directly related to her size ($n = 33$, $r_s = 0.06$, $p >> 0.05$) Among those

specimens containing measurable prey, MPS (n = 103) for males ($\bar{x}$ SVL = 148 mm) was 15.1 mm and MPS (n = 153) for females ($\bar{x}$ SVL = 132 mm) was 14.2 mm. Empty stomachs were infrequently encountered; only five males (13%) and five females (11%) had no food material in their stomachs.

Weight-length relationship

Neither the variance in SVL ($F = 0.45$, $df = 1,37$, $p >> 0.50$), nor the variance in weight ($F = 0.03$, $df = 1,37$, $p >> 0.50$), differ significantly between the 22 males and 17 females sampled. The relationship between weight and length, however, does differ between sexes ($F = 6.33$, $df = 1, 36$, $p < 0.05$). A male *L. lepida* with SVL of 148 mm (an average value for each sex within this sample) weighs between 74 and 109.5 g, while a female at 148 mm SVL weighs between 71 and 101 g. On average, when males and females are of equivalent SVL, males are 3.6% to 7.9% heavier than females.

When weight in grams is converted to cube root (y) and SVL is expressed in mm (x) the weight-length relationship in *L. lepida* from Cádiz Province, Spain, may be expressed as a linear regression formula. For males, this formula (with Standard Error in brackets) is: $y = -0.23\ (0.09) + 0.03\ (0.0006)\ x$; for females the formula is: $y = -0.09\ (0.13) + 0.03\ (0.0008)\ x$. The data from which these formulae are derived are presented graphically in fig. 4. The correlation coefficient (r) between the data and the algebraic representation of the data is 0.99 for the formula representing either sex.

Reproductive cycles

Males

Primary spermatocytes, early spermatids, and spermatozoa are most numerous in the multilayered seminiferous tubule epithelia of specimens collected from mid-April through June. Seminiferous tubules of individuals collected during July contained few spermatozoans, few spermatids, and several primary spermatocytes. These data, in addition to the presence of conspicuous cellular debris (suggestive of recent evacuation) in the tubule lumina of specimens collected in early July, suggested that mating may occur from April through July in the Cádiz population.

Lacerta lepida undergoes a refractory period. Between mid-July and mid-September seminiferous tubule diameter and lumen width are reduced, and the tubules contain only spermatogonia and Sertoli cells. While spermatogonia and Sertoli cells are present in testes throughout the year, they comprise a much greater proportion of tubule epithelia between mid-July and mid-September.

Post-breeding resumption of spermatogenesis occurs late in the year. Individuals sampled during late September demonstrated a proliferation of spermatogonia coupled with the development of primary spermatocytes. Spermatids, however, did

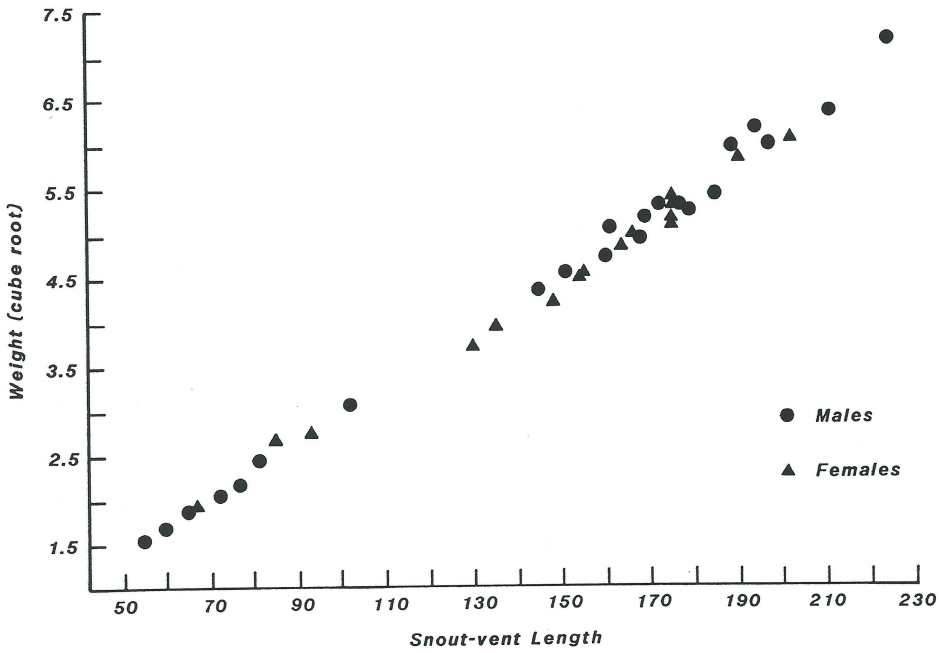

Figure 4. Weight-length relationship in *Lacerta lepida*. See text for regression data (SVL in mm).

not reappear until November. Our latest yearly sample (collected 14 November) contained numerous spermatogonia, primary spermatocytes and early spermatids.

Females

Follicular development closely parallels spermatogenic activity. Our data indicate that ovarian follicles begin maturation during April and continue developing through early July (table 5).

Egg deposition most likely occurs from early June through early July. A previously undisturbed clutch of four eggs, 21.4, 21.5, 22.6, and 23.4 mm in length (in alcohol), was uncovered in moist sand beneath a stand of *Lavandula stoechas* (Lamiales: Lamiaceae) on 13 June, and 13 and 18 shelled oviductal eggs were found in specimens collected 26 June and 5 July, respectively. The occurrence of similarly-sized developing follicles in specimens collected 23 May and 26 June (table 5) further suggests that egg laying may occur over a four week period.

Our data suggest that *L. lepida* reproduces only once a year at the southern limit of its range. No specimens collected between mid-July and 1 November appeared to demonstrate follicular development (table 5).

Table 5. Seasonal development in ovarian follicles of *L. lepida*.

date sampled	SVL (mm)	diameter of largest follicle (mm)
29 March	142.5	2.3
12 April	200.0	3.8
	191.0	2.3
23 May	137.9	9.1
	151.9	7.6
	158.2	13.6
	169.4	8.3
13 June	178.2	7.6
23 June	141.3	6.8
26 June	158.5	12.8 (shelled oviductal eggs)
5 July	210.0	17.4 (shelled oviductal eggs)
14 August	123.9	1.5
28 August	150.8	2.3
6 September	137.9	2.3
18 September	148.7	2.3
4 October	155.4	2.3
17 October	166.7	3.0
25 October	137.2	2.0
1 November	155.3	3.8

Parasitism and predation

Stomachs of these lizards contained the only internal parasite, a nematode (*Abbreviata abbreviata*; Nematoda: Physalopteridae), and eighty nematodes were found in six individuals. The one male (7 nematodes/individual) and five females (between 1 and 22 nematodes/indvidual) parasitized suggest an apparently low rate of internal parasitism (3% for males, 11% for females). The parasitized male was collected in May, two parasitized females were collected in June, and three were collected in October.

Predators include raptors, carnivorous mammals, snakes, and *L. lepida* (Valverde, 1960, 1967; Jaksić and Busack, 1984; this study). Among the raptors, the short-toed eagle (*Circaetus gallicus*), the imperial eagle (*Aquila heliaca*), the red kite and the black kite (*Milvus milvus* and *M. migrans*), bonelli's eagle and the booted eagle (*Hieraaetus faciatus* and *H. pennatus*), and the common buzzard (*Buteo buteo*) are known to feed on *L. lepida*. Other predators include the mongoose (*Herpestes ichneumon*), the red fox (*Vulpes vulpes*), the common pig (*Sus scrofa*), and the montepellier snake (*Malpolon monspessulanus*). Our study of stomach contents (table 1) demonstrates that *L. lepida* is occasionally cannibalistic.

Acknowledgements. We wish to thank A. Petter, Muséum National d'histoire Naturelle, Paris, for identification of the nematodes, C.J. McCoy and E.J. Censky, Carnegie Museum of Natural History, for the loan of specimens, and Alfredo Salvador, for assistance in the field.

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Received: August 30, 1988