Traits of reproduction and feeding of the European Green Lizard, *Lacerta viridis* (Laurenti, 1768), at the southern edge of its distribution

(Squamata: Sauria: Lacertidae)

Fortpflanzungsbiologische und nahrungsökologische Merkmale der Östlichen Smaragdeidechse *Lacerta viridis* (Laurenti, 1768) am Südrand ihres Verbreitungsgebietes
(Squamata: Sauria: Lacertidae)

Kostas Sagonas & Efstratios D. Valakos
& Petros Lymberakis & Panayiotis Pafilis

KURZFASSUNG

Die Autoren machen Angaben zur Nahrungsökologie und Reproduktion der Östlichen Smaragdeidechse, *Lacerta viridis* (Laurenti, 1768) des griechischen Festlandes, dem Südrand ihres Verbreitungsareals. Insgesamt wurden 86 Exemplare aus der herpetologischen Sammlung des Naturkundemuseums von Kreta untersucht. Die aufgenommene Nahrung wurde zu der Jahreszeit ihrer Aufnahme sowie dem Geschlecht und Alter der Smaragdeidechsen in Bezug gesetzt. Die Östliche Smaragdeidechse erwies sich als ein Nahrungsgeneralist, bei dem Coleoptera (Käfer) und Orthoptera (Springschrecken) mehr als 50 % des Mageninhalts ausmachten. Während sich die Jahreszeit nicht auf die Art der aufgenommenen Nahrung auswirkte, bestanden diesbezüglich Unterschiede zwischen den Geschlechtern und Altersklassen. Im Laufe der Ontogenese veränderte sich die Nahrungspräferenz in Richtung zu größerer und härterer Beute hin. Zudem waren Männchen vielseitiger in der Wahl der Beute und bevorzugten deutlich härtere Beute als Weibchen. Geschlechtsreife erlangten beide Geschlechter nicht unter einer Kopf-Rumpf-Länge von 70 mm. Die Fortpflanzungsaktivität beider Geschlechter erstreckte sich vom Frühling bis zur Mitte des Sommers. Die Gelegegröße variierte stark und korrelierte negativ mit dem mittleren Eivolumen des Geleges.

ABSTRACT

Information is provided on the feeding ecology and reproduction of the European Green Lizard, *Lacerta viridis* (Laurenti, 1768), from the very south of its distribution range. The authors analyzed the stomach contents of 86 preserved specimens originating from the Greek mainland stored at the Herpetological Collection of the Natural History Museum of Crete. The prey items were identified and put in relation to the season when they were eaten, and the sex and age of the lizards. In the diet of this generalist consumer, Coleoptera and Orthopera constituted more than 50 % of the total prey items in the stomach. While season had no effect on the prey taxonomic composition of the species, sex and age clearly did. *Lacerta viridis* changed its feeding preferences with maturation: adult individuals selected larger and harder prey than young, males showed a higher food niche breadth and fed on harder prey items than females. As regards to reproduction, both sexes attained sexual maturity at a snout-vent-length of more than than 70 mm. The reproductive activity of females and males lasted from early spring to mid-summer. Clutch size varied greatly and was negatively correlated with the clutch's average egg volume.

KEY WORDS

INTRODUCTION

Reproductive biology and feeding ecology are important aspects of reptilian biology and their interactions largely influence population dynamics and eventually the survival of a given species in a given place (Siliceo & Díaz 2010; Pafilis et al. 2013). The European Green Lizard, *Lacerta viridis* (Laurenti, 1768), is common in central eastern Europe (Blondel & Aronson 1999; Arnold & Ovenden 2002). The species is widespread all over the Balkans from Adriatic to the Black Sea (Naulleau 1997). Its southernmost populations are found in the mainland of Greece and

some few Greek islands (Euboea, Thasos, Samothrace and Corfu) (VALAKOS et al. 2008; PAFILIS & MARAGOU 2013).

While the phylogeny of the species was studied comprehensively (GODINHO et al. 2005; BÖHME et al. 2007; SAGONAS et al. 2014b; MARZAHN et al. 2016), its life history received comparatively limited attention (e.g., KORSÓS 1984; MOLLOV et al. 2012). In particular, no detailed studies regarding the reproduction of southern *L. viridis* are available and information on the diet are based on observations made in two small Bulgarian populations (ANGELOV et al. 1972; DONEV 1984; MOLLOV et al. 2012) and one Hungarian (KORSÓS 1984). Furthermore, these studies, because of their small sample size, provide no evidence for potential ontogenetic shifts or sexual variation in the trophic niche breadth that would provide information on intraspecific competition (ARNOLD 1987; PREEST 1994; SAGONAS et al. 2014a, 2015a).

In the present study, information on feeding and reproductive ecology of *L. viridis* from Geece was obtained at the species' southern range limit. With regard to dietary preferences, the authors hypothesize that: (i) male and female diets differ due to the larger body and head size of males that offer them access to harder and larger prey (HERREL et al. 1996; GROZDANOV & TZANKOV 2014), (ii) juveniles feed on softer prey, as a consequence of their immature head morphology and small body size (UROŠEVIĆ et al. 2013; SAGONAS et al. 2015a), and (iii) that seasonal variation in prey abundance affects the diet composition of *L. viridis* (SAGONAS et al. 2015a). As to reproduction, the study sought to provide quantitative information on male and female body size at sexual maturity, egg, clutch, and testicle volumes and sizes, and the length of the epididymis.

MATERIALS AND METHODS

Diet composition.- To identify the diet of *L. viridis* the authors dissected the digestive tracts of 86 preserved specimens (34 males, 32 females and 20 juveniles) that were stored at the Herpetological Collection of the Natural History Museum of Crete (Appendix I). From each specimen, snout-vent-length (SVL) was measured to the nearest 0.1 mm and sex and month of capture were recorded. All specimens originated from mainland Greece, viz., 11 from Sterea Ellada, 13 from Epirus, 27 from Thessaly, 28 from Macedonia and 7 from Thrace.

Stomach contents were analyzed under a binocular dissecting microscope and prey items were identified to order level. The number of prey items of each category and the presence or absence of plant material was noted down. In addition, prey items were classified on the basis of their hardness (HERREL et al. 2001; VERWAIJEN et al. 2002; SAGONAS et al. 2014a) using the categorization proposed by VANHOOYDONCK et al. (2007). Coleoptera, Gastropoda (shelled gastropods only), Isopoda, Diplopoda, and Hymenoptera were considered as hard prey;

Orthoptera, Haplotaxida (oligochaetan Annelida), Homoptera, Hemiptera and Chilopoda were classified as being of intermediate-hardness; Aranae, Opiliones, Diptera, Lepidoptera, Trichoptera and all larval forms were characterized as soft prey.

Head size variation.- Since head size and shape directly affect bite force and through this the prey consumed (HERREL et al. 2001, VERWAIJEN et al. 2002, SAGONAS et al. 2014a), five linear head characters were measured with a digital caliper (Silverline® 380244, accuracy 0.01 mm): head length (HL; measured from the tip of the snout to the posterior border of the collar), head width (HW; measured at the widest part of the head), head height (HH, measured at the highest part of the head), pileus length (PL, measured from the tip of the snout to the posterior edge of the occipital scale) and jaw length (JL, measured from the tip of the snout to the corner of the mouth). All measurements were taken twice and the average value was used (SAGONAS et al. 2014a). The geometric head size (HS) was calculated as the product of

(HL x HW x HH) (MOSIMANN 1970; SAGO-NAS et al. 2014a).

Reproduction and sexual maturity.- In males, the authors measured the longest and shortest diameter of the right testicle to calculate the testicular volume and measured the length of the epididymis, in females the numbers of vitellogenic follicles and oviductal eggs were counted and their longest and shortest axis measured to estimate their volume. The size and shape of testicles and the length of the epididymis have traditionally been used to determine sexual maturity in males, while the presence of large oviductal eggs or vitellogenic follicles (more than 4 mm in diameter) are considered indices of female maturity (TINKLE 1967; SEXTON & TURNER 1971; ADAMO-POULOU & VALAKOS 2000; SAVELIEV et al. 2006; ORTIZ et al. 2016). Clutch size was defined as the total number of oviductal eggs or the total number of vitellogenic follicles in each individual. Female specimens were also screened for signs of copulation activity (bites and scars, e.g., in the ventral side). The reproductive season in females was determined based on the presence of oviductal eggs and vitellogenic follicles. Female reproductive condition was classified as vitellogenic (yellowish yolky follicles) or ovigenous (presence of oviductal eggs). Small-sized lizards without vitellogenic follicles, oviductal eggs or enlarged testicles were considered as non-reproductive, immature individuals. All linear measurements were taken using a digital caliper (Silverline® 380244, accuracy 0.01 mm). Egg and testicle volumes were calculated by approximating the volume of an ellipsoid ($V = (4/3)\pi ab^2$, where a is half the long axis and b half the short axis (MAYHEW 1963).

Statistical analyses.- Prior to the analyses the raw and log-transformed data was examined for heteroscedasticity and normality. Whenever assumptions for parametric tests were not met, permutation tests were conducted, in the opposite case, parametric tests were used. To test for signs of sexual dimorphism in head morphology a multivariate analysis of variance (MANOVA) was employed, using the five biometric variables measured. A t-test was used to compare body size and head size between males and females.

To determine male body size at sexual maturity i.e., an SVL threshold above which the testicle volume increased, a Pearson correlation analysis between both testicle volume and length on one side, and SVL on the other, was used. This analysis included only specimens captured during the reproductive season when spermatogenesis increases the testicular volume (ADAMOPOULOU & VALAKOS 2000; VIEIRA et al. 2001; SAVELIEV et al. 2006). As body size affects linear morphometric traits, a Pearson correlation analysis was conducted to examine the existence of any relation between SVL and testicular volume in reproductive males. To test for the effect of season on the males' testicular volume, a permutation analysis of variance (perANOVA) with 999 permutations (implemented in the software PAST - HAMMER et al. 2001) was used to evaluate the differences in testicular volume between months. To examine the relation between clutch size and maternal body size, and between clutch size and mean egg volume, a Pearson correlation analysis was applied. For all statistical analyses the software package R v.3.2.3 (R DEVELOPMENT CORE TEAM 2015) was employed.

Regarding the diet, the estimates comprised the numeric percentage of each prey category found in the stomachs (% N) and the relative frequency of lizards having eaten a given taxon (F). The numbers of prey items found in the stomachs of juveniles and adults were compared using a t-test. The Shannon-Wiener diversity index (KREBS 1998) was used to calculate prey diversity (food niche breadth) (H'). A t-test was performed to test for differences in food niche breadth between age classes (adults and juveniles) and sexes (adult males and females) (ZAR 2010), while perANOVA with 999 permutations was used to test for seasonal variation. As a complementary approach, the Jaccard similarity index (JACCARD 1908) was calculated, which is not affected by the most abundant species (contrary to Shannon-Wiener index), and used to search for differences in food composition among groups of different age, sex and season. Furthermore, Pianka's overlap index (Q_{jk}) (PIANKA 1975) was calculated using the software EcoSim 7.0 (GOTELLI & ENTSMINGER 2001) to quan-

Table 1: Seasonal diet composition of male, female and juvenile *Lacerta viridis* (LAURENTI, 1768) from Greece. %N– percentage of prey items in the stomachs, F – relative frequency of individuals that ate this prey type, H' – Shannon-Wiener diversity index of prey categories. Spring – April-May, summer – June-August, autumn – September.

Tab. 1: Die saisonale Nahrungszusammensetzung bei Männchen, Weibchen und Jungtieren griechischer *Lacerta viridis* (LAURENTI, 1768). %N– Prozentsatz des Beutetyps im Magen; F – relative Häufigkeit von Individuen, welche diese Beutekategorie gefressen hatten, H' – Shannon-Wiener Diversitätsindex der Nahrungskategorien. Frühjahr – April-Mai, Sommer – Juni-August, Herbst – September.

Prey category Beutetiergruppe	Females / Weibchen						Males / Männchen						Juveniles / Jungtiere					
	Spring / Frühjahr		Summer / Sommer		Autumn / Herbst		Spring / Frühjahr		Summer / Sommer		Autumn / Herbst		Spring / Frühjahr		Summer / Sommer		Autumn / Herbst	
	F	%N	F	%N	F	%N	F	%N	F	%N	F	%N	F	%N	F	%N	F	%N
Araneae	0.29	8.33	0.17	3.57	0.29	14.29	–	–	0.11	2.25	0.40	10.00	0.25	15.38	0.30	20.00	0.67	25.00
Opiliones	0.14	8.33	0.06	2.38	0.14	9.52	–	–	0.06	3.37	–	–	–	–	0.20	8.57	0.17	6.25
Chilopoda	–	–	–	–	–	–	0.18	5.41	0.06	1.12	–	–	–	–	–	–	–	–
Orthoptera	0.43	20.83	0.61	19.05	0.57	19.05	0.27	10.81	0.22	7.87	0.60	20.00	0.25	7.69	0.50	14.29	–	–
Diplopoda	–	–	–	–	–	–	0.09	2.70	0.06	1.12	0.20	5.00	–	–	–	–	–	–
Annelida - Haplotaxida	–	–	–	–	–	–	0.18	16.22	–	–	–	–	–	–	–	–	–	–
Gastropoda	–	–	–	–	–	–	0.27	10.81	0.17	6.74	0.20	5.00	–	–	0.10	2.86	–	–
Homoptera	0.29	16.67	0.17	7.14	–	–	–	–	0.17	5.62	–	–	–	–	–	–	–	–
Hemiptera	–	–	–	–	–	–	0.09	2.70	0.06	3.37	0.20	15.00	–	–	0.10	5.71	–	–
Diptera	–	–	0.11	3.57	–	–	–	–	0.06	1.12	–	–	0.25	7.69	0.10	2.86	0.17	6.25
Isopoda	0.14	8.33	0.11	2.38	–	–	–	–	0.22	7.87	–	–	–	–	–	–	–	–
Lepidoptera	–	–	0.06	1.19	0.14	4.76	0.09	2.70	0.06	2.25	0.20	5.00	–	–	–	–	–	–
Coleoptera	0.57	33.33	0.78	41.67	0.71	28.57	0.64	43.24	0.61	41.57	0.80	35.00	0.25	7.69	0.30	8.57	0.33	12.50
Hymenoptera	–	–	0.11	4.76	–	–	–	–	0.11	3.37	–	–	–	–	0.10	5.71	0.17	18.75
Trichoptera	–	–	–	–	–	–	–	–	–	–	–	–	0.25	7.69	0.20	8.57	0.17	6.25
Formicidae	–	–	0.11	2.38	0.14	9.52	–	–	0.06	3.37	0.20	5.00	0.50	23.08	0.30	11.43	0.17	12.50
Insect larvae	0.14	4.17	0.28	11.90	0.29	14.29	0.18	5.41	0.33	8.99	–	–	0.75	30.77	0.30	11.43	0.33	12.50
Plant matter	42.86		27.78		–		36.36		22.22		20.00		25.00		–		–	
N prey items	24		84		21		37		89		20		13		35		16	
Lizard specimens	7		18		7		11		18		5		4		10		6	
Items per stomach	3.43		4.67		3.00		3.36		4.94		4.00		3.25		3.50		2.67	
Shannon-Wiener index (H')	1.75		1.83		1.82		1.75		2.10		1.80		1.78		2.26		1.96	

tify the food niche similarity between group. Chi-square tests were run to determine if there were differences in the proportion of the ingested prey taxa between sexes (males, females), age classes (adults, juveniles) and among seasons, i.e., spring (April-May), summer (June-August) and autumn (September).

RESULTS

Diet composition, its sexual, ontogenetic and seasonal variation.- The diet of *L. viridis* is composed mainly of arthropods, with Coleoptera, Orthoptera and various insect larvae being the most common prey taxa throughout the year (Table 1). Interestingly, 26 % of the specimens examined had consumed a significant amount of plant matter (e.g., seeds, leaves). The comparison of diet composition between male and female lizards revealed slight differences regarding the prey categories (Jaccard index: 0.68). These differences were mostly due to the fewer hard prey items consumed by females ($\chi^2 = 5.80$, $P < 0.01$). Diplopoda, Gastropoda and Chilopoda specifically were completely absent from female stomachs (Table 1). By contrast, female lizards selected softer prey compared to males ($\chi^2 = 5.80$, $P < 0.01$). In line with this were significant differences between sexes in the proportion of preys items selected ($\chi^2 = 36.05$, $P < 0.001$) and in niche breadth (males: H' = 2.20 and females: H' = 1.82; $t = -2.81$, $df = 266.99$, $P < 0.01$). On the other hand, there was a high food niche overlap between males and females ($Q_{jk} = 0.95$) and plant consumption was equal in both sexes (25 % vs. 26 %; $\chi^2 = 0.03$, $P = 0.50$).

The juveniles' diet differed from the diet of adult lizards (Jaccard index; females vs. juveniles: 0.57 and males vs. juveniles: 0.59) by the preference towards softer and smaller preys such as Araneae, insect larvae and Formicidae (Table 1). On the contrary, hard or intermediate hard preys such as Coleoptera, Orthoptera and Isopoda were significantly (χ^2 test; both pairwise comparisons $P < 0.05$) underrepresented (Table 1). Furthermore, plant consumption was quite limited in juveniles compared to adults (26 % vs. 5 %; $\chi^2 = 16.84$, $P < 0.001$). Consequently, food niche overlap between juveniles and adults was low (Q_{jk}; females vs. juveniles: 0.57 and males vs. juveniles: 0.48). The proportion of the different prey items consumed also differed between juveniles and adults (χ^2 test, both pairwise comparisons $P < 0.001$), whereas no difference was found in the average number of prey items per stomach ($t = 1.21$, $df = 84$, $P = 0.23$), though the adults selected for larger preys such as Orthoptera and Coleoptera. Lastly, the niche breadth of juveniles (H' = 2.22) was similar as in males ($t = -0.03$, $df = 200.88$, $P = 0.98$), but higher than in females ($t = -3.11$, $df = 184.60$, $P < 0.01$).

No seasonal divergences were detected in the proportion of prey items of adults (pairwise χ^2 tests; males and females all pairwise comparisons $P > 0.05$) or juveniles (χ^2 test; all pairwise comparisons $P > 0.05$) (Table 1). However, significant seasonal differences arose from plant consumption of males, females and juveniles who all consumed more plant matter during spring and less in autumn (χ^2 tests; all pairwise comparisons $P < 0.05$; Table 1). The food niche breadth was high at all seasons with no significant differences (all pairwise comparisons $P > 0.05$; Table 1), despite the low Jaccard similarity index between seasons (males: ~ 0.53, females ~ 0.59 and juveniles: ~ 0.67). The only exception was the higher niche breadth in juveniles during summer compared to spring (H' = 2.26 vs. 1.78). Similarly, the number of preys in the stomach of lizards showed non-significant variation during the year for the subsamples studied (ANOVA; males: $F_{2,31} = 0.60$, $P = 0.55$, females: $F_{2,29} = 0.88$, $P = 0.43$ and juveniles: $F_{2,17} = 0.46$, $P = 0.64$; Table 1).

Head and body size variation.- The comparison of SVL did not reveal any statistically significant differences between the sexes ($t = 0.34$, $df = 64$, $P = 0.73$). However, head measurements were significantly larger in males than females (MANOVA; Wilks lambda = 0.80, $F_{5,60} = 2.91$, $P = 0.020$; Table 2) for all morphometric variables tested such as, e.g., head size ($t = -2.64$, $df = 64$, $P = 0.01$; Table 2). As expected,
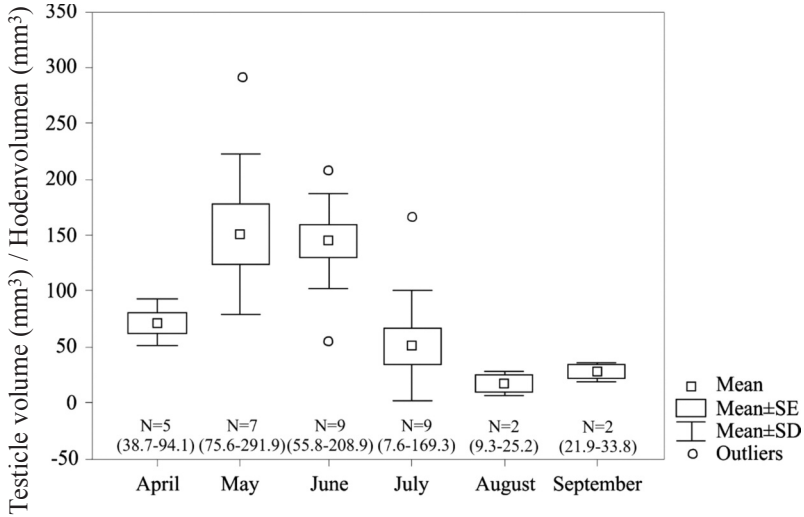
Fig. 1: Testicle volume (mm³) of Greek *Lacerta viridis* (Laurenti, 1768) in the period from April to September. SE – Standard error, SD – Standard deviation. Sample size and range in parentheses are indicated.

Abb. 1: Das Hodenvolumen (mm³) griechischer *Lacerta viridis* (Laurenti, 1768) in den Monaten April bis September. Mean – Mittelwert, SE – Standardfehler des Mittelwertes, SD – Standardabweichung. Stichprobengröße und Spannweite (in Klammern) sind angegeben.
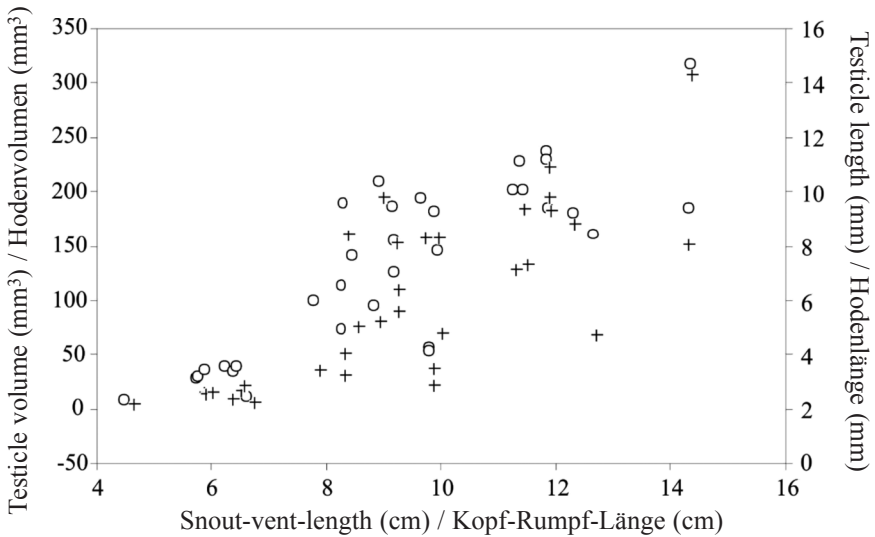

Fig. 2: Scatter plot of the relations between snout-vent-length (cm) and both testicle volume (mm³) and testicle length (mm) for 34 adult and 10 juvenile Greek specimens of *Lacerta viridis* (Laurenti, 1768), examined during the reproductive season. Observe the formation of two distinct size/age clusters below and above the 7-8 cm snout-vent-length threshold. ○ – testicle volume; + – testicle length.

Abb. 2: Streudiagramm der Beziehungen zwischen Kopf-Rumpf-Länge (cm) und Hodenvolumen (mm³) sowie Kopf-Rumpf-Länge und Hodenlänge (mm) bei 34 Erwachsenen und 10 Jungtieren griechischer *Lacerta viridis* (Laurenti, 1768) während des Fortpflanzungszeitraums. Man beachte die Ausbildung zweier Alters-/Größencluster unterhalb und oberhalb des 7-8 cm Schwellenwertes der Kopf-Rumpf-Länge, der Juvenile von geschlechtsreifen Individuen trennt. ○ – Hodenvolumen, + – Hodenlänge.

Table 2 : Descriptive statistics including mean ± standard deviation, range (minimum-maximum in parentheses) and sample size (*N*) of five head linear measurements (cm) of Greek *Lacerta viridis* (LAURENTI, 1768). SVL – Snout-vent-length, HL – Head length, HH – Head height, HW – Head width, PL – Pileus length, JL – Jaw length, HS – Geometric head size (cm³).

Tab. 2: Deskriptive Statistiken von Mittelwert ± Standardabweichung, Spannweite (Minimum-Maximum in Klammern) und Stichprobenumfang (*N*) von fünf Längenmaßen des Kopfes (cm) bei griechischen *Lacerta viridis* (LAURENTI, 1768). SVL – Kopf-Rumpf-Länge, HL – Kopflänge, HH – Kopfhöhe, HW – Kopfbreite, PL – Pileuslänge, JL – Kieferlänge, HS – Geometrisches Kopfvolumen (cm³).

Sex/Age Geschlecht/Alter	SVL	HL	HH	HW	PL	JL	HS
Females (F) Weibchen (F)	10.10 ± 1.59 (7.6 - 13.2) $N = 32$	2.87 ± 0.60 (1.7 - 4.1) N = 32	1.24 ± 0.28 (0.8 - 1.9) $N = 32$	1.44 ± 0.32 (1.0 - 2.2) $N = 32$	2.12 ± 0.42 (1.3 - 2.9) $N = 32$	1.62 ± 0.41 (0.9 - 2.5) $N = 32$	1.72 ± 0.36 (1.1 - 2.5) $N = 32$
Males (M) Männchen (M)	10.24 ± 1.72 (1.1 - 2.5) $N = 34$	3.36 ± 0.57 (2.5 - 4.9) $N = 34$	1.40 ± 0.37 (1.0 - 2.4) $N = 34$	1.67 ± 0.44 (1.1 - 3.1) $N = 34$	2.47 ± 0.46 (1.8 - 3.8) $N = 34$	1.91 ± 0.42 (1.2 - 3.4) $N = 34$	1.99 ± 0.45 (1.4 - 3.3) $N = 34$
Juveniles (J) Jungtiere (J)	5.30 ± 1.05 (3.0 - 6.6) $N = 20$	1.49 ± 0.32 (1.0 - 2.0) $N = 20$	0.72 ± 0.13 (0.5 - 0.9) $N = 20$	0.84 ± 0.13 (0.6 - 1.0) $N = 20$	1.06 ± 0.27 (0.7 - 1.6) $N = 20$	0.91 ± 0.14 (0.7 - 1.1) $N = 20$	0.96 ± 0.16 (0.7 - 1.2) $N = 20$
Statistics Statistik Groups / Gruppen	$F_{2,83} = 77.03$ $P < 0.001$ (M, F)(J)	$F_{2,83} = 77.35$ $P < 0.001$ (M)(F)(J)	$F_{2,83} = 34.98$ $P < 0.001$ (M)(F)(J)	$F_{2,83} = 36.57$ $P < 0.001$ (M)(F)(J)	$F_{2,83} = 77.94$ $P < 0.001$ (M)(F)(J)	$F_{2,83} = 46.91$ $P < 0.001$ (M)(F)(J)	$F_{2,83} = 50.01$ $P < 0.001$ (M)(F)(J)

juveniles had significantly smaller head measurements (MANOVA; Wilks lambda = 0.27, $F_{10,158} = 14.32$, $P < 0.001$), head size (ANOVA; $F_{2,83} = 50.01$, $P < 0.001$) and SVL (ANOVA; $F_{2,83} = 77.03$, $P < 0.001$) compared to adults (Table 2). To control for the effects of SVL on head size ($r = 0.92$, $P < 0.001$), the aforementioned analyses for head measurements between sexes and age groups were repeated using SVL as a covariate. Although, the differences remained (MANOVA; Wilks lambda = 0.46, $F_{10,156} = 7.52$, $P < 0.001$), a different pattern was revealed, with males and juveniles having significantly larger heads than females.

Reproduction and sexual maturity.- Spermatogenesis (assessed through the increase in testicular volume) started in April and ended in June (Fig. 1). Testicular volume reached its maximum in May (perANOVA; $P = 0.001$). Towards the end of the reproductive period (end of June), rapid reduction of the testicular volume was observed (Fig. 1). In the combined sample of adult and juvenile males the correlations between testicle volume and SVL and between testicle length and SVL were positive ($r = 0.69$, $P < 0.001$ and $r = 0.78$, $P < 0.001$; $N = 44$, respectively). Furthermore, this analysis revealed the existence of two distinct groups of males during the

reproductive season (from April to June): one comprising individuals with SVL above 80 mm whose testicles were well developed and another one below 70 mm whose testicles were not (Fig. 2 and Table 3). Also, considering adult males only, testicle volume ($r = 0.56$, $P < 0.001$; $N = 33$) and testicle length ($r = 0.58$, $P < 0.001$; $N = 33$) were positively correlated with SVL. The smallest reproductive male identified by its well developed testicles and distended epididymes (~8-10 mm length) had an SVL of 82.8 mm. Males with SVL less than 70 mm had poorly developed testicles and epididymes and therefore were sexually immature.

The percentage of sexually mature reproductive or non-reproductive females from April to September is plotted in Fig. 3. Out of the 32 adult females examined, 47 % had no eggs or follicles, 40 % were ovigenous and 13 % vitellogenic, while no female carried both vitellogenic follicles and oviductal eggs. During the reproductive period, females larger than 76 mm (the smallest mature female was 76.1 mm) bore oviductal eggs or vitellogenic follicles and had copulation signs (scars). The largest immature female examined and included in the analyses was 61.3 mm. Based on the sample available, the female reproductive

Table 3: Mean values ± standard deviation (SD) or minima for nine male and female reproductive traits of Greek *Lacerta viridis* (Laurenti, 1768).

Tab. 3: Mittelwerte ± Standardabweichung (SD) bzw. Minima von neun fortpflanzungsbiologischen Merkmalen männlicher und weiblicher *Lacerta viridis* (Laurenti, 1768) aus Griechenland.

Variable	Unit / Einheit	Mean value ± SD / Mittelwert ± SD (Minimum)	Number of individuals Anzahl Individuen
Mean Clutch size (number of vitellogenic follicles) Mittlere Gelegegröße (Anzahl dotterreiche Follikel)	- -	12.25 ± 2.75	4
Mean Clutch size (number of oviductal eggs) Mittlere Gelegegröße (Anzahl Eier im Ovidukt)	- -	12.92 ± 4.82	13
Mean Clutch volume (oviductal eggs) Mittleres Gelegevolumen (Eier im Ovidukt)	mm^3	6,944.40 ± 4,137.94	13
Mean oviductal egg volume Mittleres Volumen der Eier im Ovidukt	mm^3	530.83 ± 259.75	13
Minimum SVL reproductive female (mm) Minimale KRL reproduktiver Weibchen	mm	(76.1)	32
Minimum SVL reproductive male (mm) Minimale KRL reproduktiver Männchen	mm	(82.8)	34
Mean epididymis length Mittlere Länge des Nebenhodens	mm	14.54 ± 4.52	34
Mean testicular volume Mittleres Hodenvolumen	mm^3	95.89 ± 67.80	34
Mean testicular length Mittlere Hodenlänge	mm	7.46 ± 2.43	34

period seemed to begin during April, when the first vitellogenic follicles appeared Fig. 3. The clutch size ranged from 7 to 24 eggs. No significant correlation was found to exist between maternal SVL and (i) the number of oviductal eggs ($r = 0.19$, $P = 0.53$; $N = 13$), (ii) the number of vitellogenic follicles ($r = 0.13$, $P = 0.87$; $N = 4$), (iii) the mean oviductal egg volume ($r = 0.33$, $P = 0.23$; $N = 13$), (iv) the mean oviductal egg length ($r = 0.22$, $P = 0.44$; $N = 13$), (v) the total clutch volume ($r = 0.46$, $P = 0.11$; $N = 13$). A significant correlation between total clutch volume ($r = -0.32$, $P = 0.25$; $N = 13$) and clutch size (number of eggs) was not detected whereas, mean oviductal egg volume ($r = -0.56$, $P < 0.05$; $N = 13$) and mean egg length ($r = -0.72$, $P < 0.01$; $N = 13$) were both significantly negatively correlated with clutch size.

DISCUSSION

Feeding ecology.- *Lacerta viridis* is an actively foraging predator with wide food niche breadth (Nettmann & Rykena 1984; Arnold 1987). The presence of 17 prey categories in the diet (Table 1) reveals the lizard's opportunistic alimentary behavior, which is typical to Mediterranean lacertids (Avery 1978; Maragou et al. 1997; Valakos et al. 1997; Sagonas et al. 2015a). Independent of age class and sex, the predominant food categories were fully developed Coleoptera (34 %), Orthoptera (14 %), insect larvae (10 %) and Araneae (8 %). However, the order of preference of the four prey taxa differed between adults and juveniles. These results are in agreement with previous studies (Angelov et al. 1966; Donev 1984; Korsós 1984; Mollov et al. 2012), which identified Coleoptera, Orthoptera, larvae of Lepidoptera and Araneae as the main prey taxa of the European Green Lizard. Hymenoptera were also mentioned as an important prey of *L. viridis* (Angelov et al. 1966; Mollov et al. 2012), which is in line with the present study in which Formicidae (5 %) were singled out of the rest of Hymenoptera (4 %).

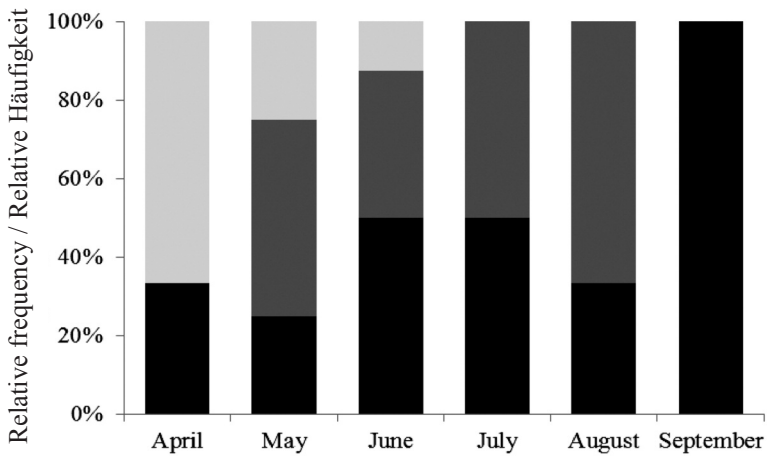Sex had a significant effect on *L. viridis* head size (Table 2), corroborating the

Fig. 3: The percentage of Greek *Lacerta viridis* (Laurenti, 1768), holding vitellogenic follicles or oviductal eggs (= reproductive females) in the period from April to September. Dark gray – females holding neither oviductal eggs nor vitellogenic follicles, medium gray – females with oviductal eggs, light gray – females with vitellogenic follicles. The synchronous presence of oviductal eggs and vitellogenic follicles was not observed.

Abb. 3 : Der Anteil griechischer *Lacerta viridis* (Laurenti, 1768), die vitellogene Follikel oder Eier enthielten (= reproduktive Weibchen) in den Monaten April bis September. Dunkelgrau – Weibchen ohne vitellogene Follikel oder Eier, mittelgrau – Weibchen mit reifen Eiern im Eileiter, hellgrau – Weibchen mit vitellogenen Follikeln. Gleichzeitige Anwesenheit von Eiern im Eileiter und vitellogenen Follikeln wurde nicht beobachtet.

typical pattern of sexual size dimorphism observed in other congeners such as *L. agilis* Linnaeus, 1758, *L. trilineata* Bedriaga, 1886, and *L. bilineata* Daudin, 1802, with males having larger heads and jaw lengths than females of similar size (Bruner et al. 2005; Urošević et al. 2013; Grozdanov & Tzankov 2014; Sagonas et al. 2014a). In lizards, head size is susceptible to various sexual selective pressures as it is associated with intraspecific competition, territorial behavior and mate success (Abouheif & Fairbairn 1997; Kwiatkowski & Sullivan 2002; Lappin & Husak 2005; Herrel et al. 2010). Moreover, head dimensions and especially head height and width are strongly associated with bite force, which in turn is linked to food choice (Herrel et al. 1999; Kaliontzopoulou et al. 2012; Sagonas et al. 2014a). By increasing head height and width males develop stronger jaw adductor muscles and thus can bite stronger compared to females (Herrel et al. 2001; Lappin & Husak 2005) which is why they can include greater proportions of hard prey in their diet increasing

their niche breadth (Herrel et al. 2001; Verwaijen et al. 2002; Sagonas et al. 2014a). The present study found a relatively low value of Jaccard's similarity index (0.68) between the preys of the sexes throughout the year. Males included in their diet harder prey (e.g., Chilopoda, Diplopoda, Gastropoda) and had a higher food niche breadth than females, indicating a less selective feeding of the former (Table 1).

Despite the sexual differences in the proportion of the consumed prey items, food niche overlap (Q_{jk} = 0.95) was high. Pianka's overlap index is strongly affected by the most abundant prey category and small sample size (Krebs 1998). Thus, the authors presume that the small sample size and the high proportion (70 %) of Coleoptera, Orthoptera and larvae in the diet are the reasons for this discrepancy.

Juveniles showed a clearly different dietary pattern from adults. Food niche overlap (Q_{jk} ~ 0.52) and Jaccard's index (~ 0.58) of dietary similarity between adults and juveniles were very low, demonstrating the ontogenetic shift in this species' feeding

preference. Juveniles exhibited a wider trophic spectrum than adult females but not wider than males. Females showed a clear preference for Coleoptera, Orthoptera and insect larvae which together represented 70 % of their diet, but avoided small and hard preys. In contrast to adults, juveniles included in their diet softer (i.e., Araneae, Trichoptera, insect larvae) and smaller (e.g., Araneae, Formicidae) preys and less plant matter (5 %). Such an ontogenetic shift in dietary preferences is common among lizards and results from the small head size and thus weaker bite force of juveniles (Herrel et al. 2006; Herrel & O'Reilly 2006). By contrast, adult males and females showed an avoidance of small prey such as Formicidae and Araneae (Table 1) and ingested plant material in considerable quantities (26 %). Herbivory and the accessory consumption of plant material in lizards are well-documented and represent an adaptation to food-scarce environments such as islands (Van Damme, 1999; Vervust et al. 2010; Dutra et al. 2011; Brock et al. 2014; Sagonas et al. 2015a). However, also the mainland populations of *L. viridis* studied here consumed significant amounts of plant material, especially seeds. To the authors' knowledge this is the first record of plant consumption for *L. viridis*, which is never reported in previous food studies (Angelov et al. 1966; Donev 1984; Korsós 1984; Mollov et al. 2012). Though plant material can accidentally be ingested while feeding on animal prey, the high proportion of adult lizards that had consumed plant material throughout the year, along with the absence of plant material in most juveniles, suggests intentional ingestion of plants.

Juveniles of the genus *Lacerta* differ from adults in their physiology, morphology and behavior, including diet (*L. bilineata*: Angelici et al. 1997; *L. agilis*: Crovetto & Salvidio 2013; *L. trilineata*: Sagonas et al. 2015a) and habitat use. They typically occur in open areas with low vegetation, whereas adults prefer wetter sites with dense vegetation cover (Arnold 1987; Angelici et al. 1997; Valakos et al. 2008). Habitat partitioning between adults and juveniles serves to reduce intraspecific competition, including aggressive behavior or cannibalism (Pafilis et al. 2009; Cooper et

al. 2014), and most important, results in the separation of the trophic niches (Angelici et al. 1997; Vitt et al. 1997; Sagonas et al. 2015a). Another explanation for the observed age-related differences in diet composition takes into account the significant ontogenetic alterations in performance and morphology of the feeding apparatus (e.g., length and digestive capability of the digestive tract, head size and bite force) that lizards undergo during growth (Durtsche 2000; Urošević et al. 2013). Since the consumption and digestion of plant material requires considerable bite force and a long digestive tract (Herrel et al. 2001; Sagonas et al. 2014a; Sagonas et al. 2015b), the low proportion of hard preys and plant matter in juvenile stomachs can be attributed to the juveniles' weaker bite force and shorter digestive tract.

The seasonal differences in the diet of *L. viridis* were not significant, regardless of age class and sex, so that the subsamples' dietary preferences remained rather stable throughout the year. In Mediterranean low altitude ecosystems, the summer is characterized by dry conditions that decrease arthropod availability (Carretero 2004) leaving fewer prey choices to lizards. As such, one would expect a decrease in food niche breadth during summer. Surprisingly, the niche breadth increased, which was statistically significant in juveniles (Table 1). In contrast to other Green Lizards which occupy dry habitats, Greek *L. viridis* live in humid places at comparatively high altitudes (Valakos et al. 2008) with more benign summers that sustains high arthropod abundance. Alternatively, one can hypothesize that the unexpectedly high food niche breadth is due to small sample size and, thus, potential underrepresentation of less common prey taxa (leaving aside the highly represented Coleoptera, Orthoptera and insect larvae that consist 70 % of the adults' diet). In agreement with the foraging theory by Stephens & Krebs (1986), the constantly high niche breadth suggests that *L. viridis* is an opportunistic predator with low food specialization. However, the patterns of plant and insect consumption were significantly different within the year: the frequency of plant material in stomachs decreased gradually from spring and summer

when seeds are abundant to autumn (Table 1). The above results corroborate those of previous researchers (e.g., ANGELOV et al. 1972; NETTMANN & RYKENA 1984; MOLLOV et al. 2012) and provide further information on the impact of season, sex and age on the diet of the species.

R e p r o d u c t i v e   t r a i t s .- Body size (SVL) is frequently used as a reliable indicator of sexual maturity in lizards (RUBY & DUNHAM 1985; GALÁN, 1996; IN DEN BOSCH & BOUT 1998; VITT & CALDWELL 2014), Green Lizards included (ARNOLD 1987; ANGELICI et al. 1997; AMAT et al. 2000; PAFILIS & VALAKOS 2008). In the present study Greek *L. viridis* with SVL below 70 mm were clearly sexually immature and the minimum size for the initiation of reproductive activity was 76.1 mm SVL for females and 82.8 mm for males (Table 2). These results are in agreement with the 70-80 mm threshold that has been set to distinguish adults from juveniles in *L. bilineata*, sister species of *L. viridis* (SAINT GIRONS et al. 1989; BÖHME et al. 2007; SAGONAS et al. 2014b), *L. trilineata* (ARNOLD 1987; PAFILIS & VALAKOS 2008), *L. agilis* (AMAT et al. 2000; ROITBERG & SMIRINA 2006; but see DUDEK et al. 2014) and *L. strigata* EICHWALD, 1831 (ROITBERG & SMIRINA 2006).

Lacerta viridis emerges from hibernation in March/April and ends the active phase in October/November (VACLAV et al. 2007; REHÁK 2015), its reproductive period beginning in April with spermatogenesis in males and the formation of vitellogenic follicles in females and ending in early August with oviposition. During this time, food availability can be an important factor influencing the reproductive success of lizards (BRADSHAW et al. 1991; PAFILIS et al. 2011; RAMOS-PALLARES et al. 2015) since spermatogenesis and courtship in males and oogenesis in females are energy-consuming processes that require significant amounts of nutrients (BRADSHAW et al. 1991; VITT & CALDWELL 2014). The observed increase in food niche breadth during June and July may be associated with the increased energy required.

The variation in the reproductive output of female *L. viridis* was considerable. The number of eggs per clutch ranged from 7 to 24 (Table 3). Although no female was found which carried both oviductal eggs and vitellogenic follicles at the same time, previous studies have reported that the species can produce as much as two clutches per year: the first in June and the second in July (REHÁK 2015). The small sample size of reproductive females examined may account for the absence of evidence. Interestingly, a significant correlation between egg number (clutch size) or clutch volume and maternal body size was not established, which might be due to small sample effects as the correlation coefficient in both cases was relative high. However, egg volume, but not total clutch volume, was negatively correlated with clutch size. The latter finding suggests that *L. viridis* has reached a physiologically maximum clutch volume, but not in egg number (clutch size), probably as a result of the limitations of the space available in the females' abdominal cavity (ADAMOPOULOU & VALAKOS 2000; PAFILIS et al. 2011). The negative correlation observed between clutch size and clutch volume is likely another evidence of this space limitation.

REFERENCES

ABOUHEIF, E. & FAIRBAIRN, D. J. (1997): A comparative analysis of allometry for sexual size dimorphism: Assessing Rensch's rule.- The American Naturalist, Chicago; 149: 540-562.

ADAMOPOULOU, C. & VALAKOS, E. (2000): Small clutch size in a Mediterranean endemic lacertid (*Podarcis milensis*).- Copeia, Washington; 2000: 610-614.

AMAT, F. O. & LLORENTE, G. A. & CARRETERO, M. A. (2000): Reproductive cycle of the sand lizard (*Lacerta agilis*) in its southwestern range.- Amphibia-Reptilia, Leiden; 21: 463-476.

ANGELICI, F. M. & LUISELLI, L. & RUGIERO, L. (1997): Food habits of the green lizard, *Lacerta bilineata*, in central Italy and a reliability test of faecal pellet analysis.- Italian Journal of Zoology, London; 64: 267-272.

ANGELOV, P. & GRUEV, B. & TOMOV, V. (1972): Studies on the food of the Green Lizard *Lacerta viridis* LAUR. in Bulgaria.- Naucni trudove / Biologija / Plovdivski Universitet Paisij Chilendarski, Plovdiv; 10 (1): 155-161. [in Bulgarian]

ANGELOV, P. & TOMOV, V. & GRUEV, B. (1966): Izsledvaniia vyrhu hranata na niakoi vidove gushteri v Bulgaria [A study on the diet of some lizards in Bulgaria].- Nauchni Trudove na Visshiia Pedagogicheski Institut Plovdiv - Biologija, Plovdiv; 4 (3): 99-105. [In Bulgarian, Russian summary]

ARNOLD, E. N. (1987): Resource partition among lacertid lizards in southern Europe.- Journal of Zoology, London; 1: 739-782.

ARNOLD, E. N. & OVENDEN, D. W. (2002): Reptiles and amphibians of Europe. Princeton (Princeton University Press), pp. 288.

AVERY, R. A. (1978): Activity patterns, thermoregulation and food consumption in two sympatric lizard species (*Podarcis muralis* and *P. sicula*) from central Italy.- Journal of Animal Ecology, London; 47: 143-158.

BLONDEL, J. & ARONSON, J. (1999): Biology and wildlife of the Mediterranean region. New York (Oxford University Press), pp. 328.

BÖHME, M. U. & FRITZ, U. & KOTENKO, T. & DŽUKIĆ, G. & LJUBISAVLJEVIĆ, K. & TZANKOV, N. & BERENDONK, T. U. (2007): Phylogeography and cryptic variation within the *Lacerta viridis* complex (Lacertidae, Reptilia).- Zoologica Scripta, Oslo; 36: 119-131.

BRADSHAW, S. D. & SAINT GIRONS, H. & BRADSHAW, F. J. (1991): Seasonal changes in material and energy balance associated with reproduction in the green lizard, *Lacerta viridis*, in western France.- Amphibia-Reptilia, Leiden; 12: 21-32.

BROCK, K. M. & DONIHUE, C. M. & PAFILIS, P. (2014): New records of frugivory and ovophagy in *Podarcis* (Lacertidae) lizards from East Mediterranean Islands.- North-Western Journal of Zoology, Oradea; 10: 223-225.

BRUNER, E. & COSTANTINI, D. & FANFANI, A. & DELL'OMO, G. (2005): Morphological variation and sexual dimorphism of the cephalic scales in *Lacerta bilineata*.- Acta Zoologica, Stockholm; 86: 245-254.

CARRETERO, M. A. (2004): From set menu to à la carte. Linking issues in trophic ecology of Mediterranean lacertids.- Italian Journal of Zoology, London; 2: 121-133.

COOPER, J. W. E. & DIMOPOULOS, I. & PAFILIS, P. (2014): Sex, age and population density affect aggressive behaviors in island lizards promoting cannibalism.- Ethology, Berlin; 121: 260-269.

CROVETTO, F. & SALVIDIO, S. (2013): Feeding habits of the sand lizard, *Lacerta agilis*, from North-Western Italian Alps.- Folia Zoologica, Brno; 62: 264-268.

DONEV, A. (1984): Studies on the food of the Green Lizard *Lacerta viridis* Laur.- Naucni trudove / Biologija / Plovdivski Universitet Paisij Chilendarski, Plovdiv; 22: 121-126. [in Bulgarian].

DUDEK, K. & SAJKOWSKA, Z. & GAWAŁEK, M. & EKNER-GRZYB, A. (2014): Using body condition index can be an unreliable indicator of fitness: a case of sand lizard *Lacerta agilis* LINNAEUS, 1758 (Sauria: Lacertidae).- Turkish Journal of Zoology, Ankara; 39: 182-184.

DURTSCHE, R. D. (2000): Ontogenetic plasticity of food habits in the Mexican spiny-tailed iguana, *Ctenosaura pectinata*.- Oecologia, Heidelberg; 124: 185-195.

DUTRA, G. F. & SIQUEIRA, C. C. & VRCIBRADIC, D. & KIEFER, M. C. & ROCHA, C. F. D. (2011): Plant consumption of insular and mainland populations of a tropical lizard.- Herpetologica, Lawrence; 67 (1): 32-45.

GALÁN, P. (1996): Sexual maturity in a population of the lacertid lizard *Podacis bocagei*.- Herpetological Journal, London; 6: 87-93.

GODINHO, R. & CRESPO, E. G. & FERRAND, N. & HARRIS, D. J. (2005): Phylogeny and evolution of the green lizards, *Lacerta* spp. (Squamata: Lacertidae) based on mitochondrial and nuclear DNA sequences.- Amphibia-Reptilia, Leiden; 26: 271-285.

GOTELLI, N. J. & ENTSMINGER, G. L. (2001): EcoSim: Null Models Software for Ecology, Version 7.0. Montrose. WWW document and software available at < http://homepages.together.net/~gentsmin/ecosim.htm> (Acquired Intelligence Inc. & Kesey-Bear).

GROZDANOV, A. P. & TZANKOV, N. D. (2014): Analysis and comparison of sexual size dimorphism in two lacertid species in Bulgaria.- Bulgarian Journal of Agricultural Science, Sofia; 20: 139-142.

HAMMER, Ø. & HARPER, D. A. T. & RYAN, P. D. (2001): PAST: Paleontological Statistics software package for education and data analysis.- Palaeontologia Electronica, California; 4: 1-9. WWW document and software available at < https://folk.uio.no/ohammer/past/ >.

HERREL, A. & JOACHIM, R. & VANHOOYDONCK, B. & IRSCHICK, D. J. (2006): Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*.- Biological Journal of the Linnean Society, London; 89: 443-454.

HERREL, A. & MOORE, J. A. & BREDEWEG, E. M. & NELSON, N. J. (2010): Sexual dimorphism, body size, bite force and male mating success in tuatara.- Biological Journal of the Linnean Society, London; 100: 287-292.

HERREL, A. & O'REILLY, J. C. (2006): Ontogenetic scaling of bite force in lizards and turtles.- Physiological and Biochemical Zoology, Chicago; 79: 31-42.

HERREL, A. & SPITHOVEN, L. & VAN DAMME, R. & DE VREE, F. (1999): Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses.- Functional Ecology, London; 13: 289-297.

HERREL, A. & VAN DAMME, R. & DE VREE, F. (1996): Sexual dimorphism of head size in *Podarcis hispanica atrata*: Testing the dietary divergence hypothesis by bite force analysis.- Netherlands Journal of Zoology, Leiden; 46: 253-262.

HERREL, A. & VAN DAMME, R. & VANHOOYDONCK, B. & DE VREE, F. (2001): The implications of bite performance for diet in two species of lacertid lizards.- Canadian Journal of Zoology, Ottawa; 79: 662-670.

IN DEN BOSCH, H. A. J. & BOUT, R. G. (1998): Relationships between maternal size, egg size, clutch size, and hatchling size in European lacertid lizards.- Journal of Herpetology, Houston etc.; 32: 410-417.

JACCARD, P. (1908): Nouvelles recherches sur la distribution florale.- Bulletin de la Société Vaudoise des Sciences Naturelles, Lausanne; 44: 223-270.

KALIONTZOPOULOU, A. & ADAMS, D. C. & VAN DER MEIJDEN, A. & PERERA, A. & CARRETERO, M. A. (2012): Relationships between head morphology, bite performance and ecology in two species of *Podarcis* wall lizards.- Evolutionary Ecology, London; 26: 825-845.

KREBS, C. J. (1998): Ecological Methodology. New York (Harper Collins), pp. 620.

KORSÓS, Z. (1984): Comparative niche analysis of two sympatric lizard species (*Lacerta viridis* and *Lacerta agilis*).- Vertebrata hungarica, Budapest; 22: 5-14.

KWIATKOWSKI, M. A. & SULLIVAN, B. K. (2002): Geographic variation in sexual selection among populations of an iguanid lizard, *Sauromalus obesus* (=*ater*).- Evolution, Hoboken; 56: 2039-2051.

LAPPIN, A. K. & HUSAK, J. F. (2005): Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*).- The American Naturalist, Chicago; 166: 426-436.

MARAGOU, P. & VALAKOS, E. D. & CHONDRO-POULOS, B. (1997): Comparative ecology of two sympatric lizard species, *Lacerta graeca* and *Podarcis peloponnesiaca* (Sauria: Lacertidae) endemic to Peloponnisos (Greece); pp. 265-271. In: BÖHME, W. & BISCHOFF, W. & ZIEGLER, T. (Eds.): Herpetologia Bonnensis, Proceedings of the 8th Ordinary General Meeting of the Societas Europaea Herpetologica, 23-27 August 1995 in Bonn, Germany. Bonn (SEH).

MARCO, A. & PÉREZ-MELLADO, V. & GIL-COSTA, M. J. (1994): Reproductive strategy in a montane population of the lizard *Lacerta schreiberi* (Sauria: Lacertidae).- Herpetological Journal, London; 4: 49-55.

MARZAHN, E. & MAYER, W. & JOGER, U. & ILGAZ, C. & JABLONSKI, D. & KINDLER, C. & KUM-LUTAŞ, Y. & NIŞTRI, A. & SCHNEEWEISS, N. & VAMBERGER, M. & ŽAGAR, A. & FRITZ, U. (2016): Phylogeography of the *Lacerta viridis* complex: Mitochondrial and nuclear markers provide taxonomic insights.- Journal of Zoological Systematics and Evolutionary Research, Berlin; 54: 85-105.

MAYHEW, W. W. (1963): Reproduction in the granite spiny lizard, *Sceloporus orcutti*.- Copeia, Washington; 1963: 144-152.

MOLLOV, I. & BOYADZHIEV, P. & DONEV, A. (2012): Trophic niche breadth and niche overlap between two lacertid lizards (Reptilia: Lacertidae) from south Bulgaria.- Acta Zoologica Bulgarica, Sofia; Suppl. 4: 129-136.

MOSIMANN, J. E. (1970): Size and shape variables with characterizations of the lognormal and generalized gamma distributions.- Journal of the American Statistical Association, Washington; 65: 930-945.

NAULLEAU, G. (1997): *Lacerta viridis* (LAUREN-TI, 1768); pp. 266–267. In: GASC, J. P. & CABELA, A. & CRNOBRNJA-ISAILOVIC, J. & DOLMEN, D. & GROSSEN-BACHER, K. & HAFFNER, P. & LESCURE, J. & MARTENS, H. & MARTINEZ-RICA, J. P. & MAURIN, H. & OLIVEIRA, M. E. & SOFIANIDOU, T. S. & VEITH, M. & ZUIDERWIJK, A. (Eds.): Atlas of amphibians and reptiles in Europe; Paris (Societas Europaea Herpetologica / Muséum National d'Histoire Naturelle).

NETTMANN, H. K. & RYKENA, S. (1984): *Lacerta viridis* (LAURENTI, 1768) - Smaragdeidechse; pp. 129-180. In: BÖHME, W. (Ed.): Handbuch der Reptilien und Amphibien Europas, Echsen (Sauria) II; Wiesbaden (AULA-Verlag).

ORTIZ, M. A. & BORETTO, J. M. & IBARGÜEN-GOYTÍA, N. R. (2016): Reproductive biology of the southernmost *Kentropyx* lizard from the Wet Chaco of Corrientes, Argentina.- Herpetological Journal, London; 26: 119-130.

PAFILIS, P. & ANASTASIOU, I. & SAGONAS, K. & VALAKOS, E. D. (2013): Grazing by goats on islands affects the populations of an endemic Mediterranean lizard.- Journal of Zoology, London; 290: 255-264.

PAFILIS, P. & FOUFOPOULOS, J. & SAGONAS, K. & RUNEMARK, A. & SVENSSON, E. & VALAKOS, E. D. (2011): Reproductive biology of insular reptiles: Marine subsidies modulate expression of the "Island Syndrome".- Copeia, Washington; 2011: 545-552.

PAFILIS, P. & MARAGOU, P. (2013): One more record of *Lacerta viridis* (LAURENTI, 1768), from Macedonia.- Herpetozoa, Wien; 26: 101-102.

PAFILIS, P. & MEIRI, S. & FOUFOPOULOS, J. & VALAKOS, E. (2009): Intraspecific competition and high food availability are associated with insular gigantism in a lizard.- Naturwissenschaften, Heidelberg; 96: 1107-1113.

PAFILIS, P. & VALAKOS, E. D. (2008): Loss of caudal autotomy during ontogeny of Balkan green lizard, *Lacerta trilineata*.- Journal of Natural History, London; 42: 409-419.

PIANKA, E. R. (1975): Niche relation of desert lizards; pp. 292-314. In: GODY, M. & DIAMOND, J. (Eds.): Ecology and evolution of communities; Harvard University Press (Cambridge).

PREEST, M. R. (1994): Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: Why do females take smaller prey than males?- Journal of Herpetology, Houston etc.; 28: 292-294.

R DEVELOPMENT CORE TEAM (2015): R: a language and environment for statistical computing. Vienna (R Foundation for Statistical Computing). WWW document and software available at < https://www.r-project.org >.

RAMOS-PALLARES, E. & ANAYA-ROJAS, J. M. & SERRANO-CARDOZO, V. H. & RAMÍREZ-PINILLA, M. P. (2015): Feeding and reproductive ecology of *Bachia bicolor* (Squamata: Gymnophthalmidae) in urban ecosystems from Colombia.- Journal of Herpetology, Houston etc.; 49: 108-117.

REHÁK, I. (2015): Protecting and managing a local population of the European Green lizard *Lacerta viridis* at the Prague Zoo, Czech Republic.- International Zoo Yearbook, London; 49: 56-66.

ROITBERG, E. S. & SMIRINA, E. M. (2006): Age, body size and growth of *Lacerta agilis boemica* and *L. strigata*: a comparative study of two closely related lizard species based on skeletochronology.- Herpetological Journal, London; 16: 133-148.

RUBY, D. E. & DUNHAM, A. E. (1985): A population analysis of the ovoviviparous lizard *Sceloporus*

jarrovi in the Pifialeño mountains of southeastern Arizona.- Herpetologica, Lawrence; 40: 425-436.

SAGONAS, K. & PAFILIS, P. & LYMBERAKIS, P. & DONIHUE, C. M. & HERREL, A. & VALAKOS, E. D. (2014a): Insularity affects head morphology, bite force and diet in a Mediterranean lizard.- Biological Journal of the Linnean Society, London; 112: 469-484.

SAGONAS, K. & PAFILIS, P. & LYMBERAKIS, P. & VALAKOS, E. D. (2015a): Trends and patterns in the feeding ecology of the widespread Balkan lizard *Lacerta trilineata* (Squamata: Lacertidae) in insular and continental Greece.- North-Western Journal of Zoology, Oradea; 11: 117-126.

SAGONAS, K. & PAFILIS, P. & VALAKOS, E. D. (2015b): Effects of insularity on digestive performance: living in islands induces shifts in physiological and morphological traits in a Mediterranean lizard?- The Science of Nature, Heidelberg; 102: 55-62.

SAGONAS, K. & POULAKAKIS, N. & LYMBERAKIS, P. & PARMAKELIS, A. & PAFILIS, P. & VALAKOS, E. D. (2014b): Molecular systematics and historical biogeography of the green lizards (*Lacerta*) in Greece: Insights from mitochondrial and nuclear DNA.- Molecular Phylogenetics and Evolution, Amsterdam; 76: 144-154.

SAINT GIRONS, H. & CASTANET, J. & BRADSHAW, S. D. & BARON, J. P. (1989): Démographie comparée de deux populations françaises de *Lacerta viridis* (LAURENTI, 1768).- Revue d'Écologie, Paris; 44: 361-386.

SEXTON, O. J. & TURNER, O. (1971): The reproductive cycle of a neotropical lizard.- Ecology, Washington; 52: 159-164.

SILICEO, I. & DÍAZ, J. A. (2010): A comparative study of clutch size, range size, and the conservation status of island vs. mainland lacertid lizards.- Biological Conservation, Barking; 143: 2601-2608.

STEPHENS, D. W. & KREBS, J. R. (1986): Foraging Theory; Princeton (Princeton University Press), pp. 262.

TINKLE, D. W. (1967): The life and demography of the side blotched lizard, *Uta stansburiana*. Ann Arbor (Museum of Zoology, University of Michigan), pp. 188.

UROŠEVIĆ, A. & LJUBISAVLJEVIĆ, K. & IVANOVIĆ, A. (2013): Patterns of cranial ontogeny in lacertid lizards: Morphological and allometric disparity.- Journal of Evolutionary Biology, Oxford; 26: 399-415.

VACLAV, R. & PROKOP, P. & FEKIA, V. (2007): Expression of breeding coloration in European Green Lizards (*Lacerta viridis*): variation with morphology and tick infestation.- Canadian Journal of Zoology, Ottawa; 85: 1199-1206.

VALAKOS, E. D. & ADAMOPOULOU, C. & MARAGOU, P. & MYLONAS, M. (1997): The food of

Podarcis milensis and *Podarcis erhardii* in the insular ecosystems of the Aegean; pp. 373-381. In: BÖHME, W. & BISCHOFF, W. & ZIEGLER, T. (Eds.): Herpetologia Bonnensis, Proceedings of the 8th Ordinary General Meeting of the Societas Europaea Herpetologica, 23-27 August 1995 in Bonn, Germany. Bonn (SEH).

VALAKOS, E. D. & PAFILIS, P. & SOTIROPOULOS, K. & LYMBERAKIS, P. & MARAGOU, P. & FOUFOPOULOS, J. (2008): The Amphibians and Reptiles of Greece. Frankfurt am Main (Chimaira), pp. 465. [Frankfurt Contributions to Natural History No. 32]

VANCEA, ST. & FUHN, I. E. (1959): Contributions à la systématique et à l'écologie des lacertides de la R.P.R. II. Le lézard vert de bois - *Lacerta viridis* LAURENTIUS [sic].- Annales Scientifiques de l'Université de Jassy, Jassy; (N. S., Sec. 2): 5 (1): 61-80.

VAN DAMME, R. (1999): Evolution of herbivory in lacertid lizards: effects of insularity and body size.- Journal of Herpetology, Houston etc.; 33: 663-674.

VANHOOYDONCK, B. & HERREL, A. & VAN DAMME, R. (2007): Interactions between habitat use, behavior and the trophic niche of lacertid lizards; pp. 427-449. In: REILLY, S. M. & MCBRAYER, L. D. & MILES, D. B. (Eds.): Lizard ecology: The evolutionary consequences of foraging mode; Cambridge (Cambridge University Press).

VERVUST, B. & PAFILIS, P. & VALAKOS, E. D. & VAN DAMME, R. (2010): Anatomical and physiological changes associated with a recent dietary shift in the lizard *Podarcis sicula*.- Physiological and Biochemical Zoology, Chicago; 83: 632-642.

VERWAIJEN, D. & VAN DAMME, R. & HERREL, A. (2002): Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards.- Functional Ecology, London; 16: 842-850.

VIEIRA, G. H. C. & WIEDERHECKER, H. & COLLI, G. & BÁO, S. (2001): Spermiogenesis and testicular cycle of the lizard *Tropidurus torquatus* (Squamata, Tropiduridae) in the Cerrado of central Brazil.- Amphibia-Reptilia, Leiden; 22: 217-233.

VITT, L. J. & CALDWELL, J. P. (2014): Herpetology: An introductory biology of amphibians and reptiles, Fourth edition. London, UK (Academic Press), pp. 713.

VITT, L. J. & ZANI, P. A. & MONTEIRO DE BARROS, A. A. (1997): Ecological variation among populations of the gekkonid lizard *Gonatodes humeralis* in the Amazon basin.- Copeia, Washington; 1997: 32-43.

ZAR, J. H. (2010): Biostatistical analysis. Upper Saddle River (Prentice Hall Inc.), pp. 947.

Appendix I

Museum specimens of *Lacerta viridis* (LAURENTI, 1768) from Greece used in this study. Origin, age class, sex and date of collection are indicated. NHMC - Natural History Museum of Crete, a - adult, j - juvenile, M - male, F - female. / In der vorliegenden Untersuchung verwendete Museumsexemplare von *Lacerta viridis* (LAURENTI, 1768) aus Griechenland. Herkunft, Altersklasse, Geschlecht und Sammeldatum sind angegeben. NHMC - Natural History Museum of Crete, a - adult, j - juvenil, M - Männchen, F - Weibchen.

Museum Number / Inventarnummer	Region	Age, sex Alter, Sex	Date Datum	Museum Number / Inventarnummer	Region	Age, sex Alter, Sex	Date Datum
NHMC80.3.61.1	Macedonia	a, F	95-07-08	NHMC80.3.61.2	Sterea Ellada	a, F	95-07-04

Museum Number / Inventarnummer	Region	Age, sex / Alter, Sex	Date Datum	Museum Number / Inventarnummer	Region	Age, sex / Alter, Sex	Date Datum
NHMC80.3.61.3	Thessaly	a, M	02-07-06	NHMC80.3.61.61	Thrace	j, M	08-06-01
NHMC80.3.61.4	Macedonia	j, F	99-09-30	NHMC80.3.61.62	Thrace	j, F	09-04-14
NHMC80.3.61.5	Macedonia	j, F	96-07-07	NHMC80.3.61.63	Thrace	a, F	09-04-14
NHMC80.3.61.6	Macedonia	j, M	99-09-30	NHMC80.3.61.64	Thessaly	a, F	10-09-18
NHMC80.3.61.13	Thessaly	a, F	01-07-29	NHMC80.3.61.65	Macedonia	a, M	09-04-13
NHMC80.3.61.14	Thessaly	a, M	01-07-28	NHMC80.3.61.67	Thrace	a, M	09-05-22
NHMC80.3.61.15	Thessaly	a, M	01-07-30	NHMC80.3.61.71	Sterea Ellada	a, M	08-07-03
NHMC80.3.61.16	Macedonia	a, F	96-07-07	NHMC80.3.61.72	Sterea Ellada	a, F	08-07-03
NHMC80.3.61.20	Thessaly	a, F	01-07-30	NHMC80.3.61.75	Thessaly	a, M	10-04-05
NHMC80.3.61.21	Thessaly	a, M	01-07-30	NHMC80.3.61.78	Macedonia	a, M	10-05-23
NHMC80.3.61.22	Sterea Ellada	a, M	98-07-04	NHMC80.3.61.79	Epirus	j, M	10-09-11
NHMC80.3.61.23	Macedonia	j, F	99-06-21	NHMC80.3.61.80	Epirus	j, F	10-09-14
NHMC80.3.61.24	Macedonia	a, F	01-04-15	NHMC80.3.61.81	Epirus	a, M	10-05-29
NHMC80.3.61.25	Macedonia	a, F	93-05-07	NHMC80.3.61.82	Epirus	a, M	10-06-26
NHMC80.3.61.26	Epirus	a, F	01-06-13	NHMC80.3.61.83	Epirus	a, M	10-09-14
NHMC80.3.61.27	Thrace	a, F	99-09-13	NHMC80.3.61.84	Thessaly	a, F	10-09-15
NHMC80.3.61.28	Thrace	a, F	99-09-13	NHMC80.3.61.85	Thessaly	a, F	10-07-19
NHMC80.3.61.29	Macedonia	a, F	99-06-18	NHMC80.3.61.86	Macedonia	j, M	10-06-20
NHMC80.3.61.30	Macedonia	a, M	99-06-18	NHMC80.3.61.87	Sterea Ellada	a, M	10-09-11
NHMC80.3.61.31	Macedonia	a, M	99-05-23	NHMC80.3.61.90	Thessaly	a, M	11-05-16
NHMC80.3.61.32	Macedonia	a, F	99-09-12	NHMC80.3.61.91	Macedonia	a, M	11-06-22
NHMC80.3.61.33	Macedonia	a, F	99-05-23	NHMC80.3.61.92	Sterea Ellada	a, M	11-06-15
NHMC80.3.61.35	Macedonia	j, M	99-09-12	NHMC80.3.61.94	Epirus	a, M	11-06-08
NHMC80.3.61.36	Macedonia	a, M	99-09-12	NHMC80.3.61.95	Epirus	a, F	11-07-08
NHMC80.3.61.37	Macedonia	j, F	82-05-28	NHMC80.3.61.96	Macedonia	a, M	11-09-19
NHMC80.3.61.38	Thessaly	j, M	04-06-27	NHMC80.3.61.97	Macedonia	j, M	11-06-01
NHMC80.3.61.40	Thessaly	a, M	04-06-28	NHMC80.3.61.98	Macedonia	a, F	11-05-31
NHMC80.3.61.43	Sterea Ellada	a, M	04-05-20	NHMC80.3.61.99	Thessaly	a, F	11-06-10
NHMC80.3.61.44	Epirus	a, F	05-07-05	NHMC80.3.61.100	Macedonia	a, F	11-06-24
NHMC80.3.61.45	Epirus	a, F	05-07-05	NHMC80.3.61.101	Macedonia	a, F	11-06-24
NHMC80.3.61.46	Epirus	a, M	05-07-05	NHMC80.3.61.105	Macedonia	j, M	11-06-23
NHMC80.3.61.48	Epirus	a, F	05-07-06	NHMC80.3.61.106	Thessaly	a, M	11-06-06
NHMC80.3.61.49	Epirus	a, M	05-07-04	NHMC80.3.61.107	Thessaly	a, F	11-05-06
NHMC80.3.61.50	Sterea Ellada	a, M	05-05-20	NHMC80.3.61.111	Thessaly	j, F	11-07-14
NHMC80.3.61.51	Thrace	j, F	05-09-20	NHMC80.3.61.112	Thessaly	j, F	11-06-13
NHMC80.3.61.52	Sterea Ellada	a, M	06-04-14	NHMC80.3.61.113	Thessaly	a, M	11-06-13
NHMC80.3.61.53	Thessaly	j, F	06-04-14	NHMC80.3.61.114	Thessaly	a, M	11-07-14
NHMC80.3.61.54	Sterea Ellada	a, M	05-06-20	NHMC80.3.61.118	Thessaly	j, M	11-07-10
NHMC80.3.61.55	Thessaly	a, M	06-09-03	NHMC80.3.61.119	Macedonia	a, F	11-09-05
NHMC80.3.61.57	Thessaly	a, F	06-09-17	NHMC80.3.61.120	Macedonia	a, F	11-07-09
NHMC80.3.61.58	Thessaly	j, M	06-05-30	NHMC80.3.61.136	Sterea Ellada	a, F	11-05-08
NHMC80.3.61.60	Thessaly	a, F	07-06-03	NHMC80.3.61.137	Thessaly	a, M	11-05-06

AUTHORS: Kostas SAGONAS (Corresponding author < ksagonas@biol.uoa.gr >) [1, 2], Efstratios D. VALAKOS [2], Petros LYMBERAKIS [3] & Panayiotis PAFILIS [4]

[1]. School of Biological and Chemical Sciences, Queen Mary University of London, E1 4NS London, UK.
[2] Department of Human and Animal Physiology, Faculty of Biology, National and Kapodistrian University of Athens, Panepistimioupolis Zografou, 15784 Athens, Greece.
[3] Natural History Museum of Crete, University of Crete, Knossos Ave, P.O. Box 2208, 71409 Irakleio, Crete, Greece.
[4] Department of Zoology and Marine Biology, Faculty of Biology, National and Kapodistrian University of Athens, Panepistimioupolis Zografou, 15784 Athens, Greece.