NORTH-WESTERN JOURNAL OF ZOOLOGY 11 (1): 117-126 ©NwjZ, Oradea, Romania, 2015
Article No.: 141510 *http://biozoojournals.ro/nwjz/index.html*

Trends and patterns in the feeding ecology of the widespread Balkan green lizard *Lacerta trilineata* (Squamata: Lacertidae) in insular and continental Greece

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Received: 16. January 2014 / Accepted: 08. November 2014 / Available online: 03. January 2015 / Printed: June 2015

Abstract. The Balkan green lizard (*Lacerta trilineata*) is the most widespread lizard in the Balkans, ranging from Croatia to Crete and from Ionian to Black Sea. Surprisingly, its feeding ecology remains largely understudied. In this study we describe the diet of the species using 288 specimens from museum collections that derived from 8 island and 4 mainland populations from Greece. Besides yielding basic information on the trophic preferences of the species, our aim was also to unravel the effect of sex, age, season and habitat on the feeding patterns. The diet of *L. trilineata* consisted mainly of insects, with Coleoptera (51%) and Orthoptera (11%) being the predominant prey groups. Though we failed to detect any sexual variation, we found that ontogeny, season and habitat seem to affect the feeding ecology of the species. Juveniles had higher niche breadth and fed on softer preys. *Lacerta trilineata* changes its feeding preferences throughout the year. Island populations adopted a higher niche breadth during summer; mainland lizards – during spring. Islanders showed also a clear proneness to herbivory, most probably due to the food scarcity of the islands. *Lacerta trilineata* is an opportunistic predator that shifts its diet according to season and habitat.

Key words: *Lacerta trilineata*, trophic ecology, niche breadth, Greece, ontogeny, islands.

Introduction

Feeding ecology is an important field in reptilian studies, yielding valuable information that improves our understanding on how reptiles exploit their environment (Pitt & Ritchie 2002, Pincheira-Donoso 2008). Food preferences are closely related to numerous biology dynamics such as sexual selection, energy flow, digestive physiology and bite performance (Andersson 1994, Pafilis et al. 2007, Herrel et al. 2008, Kaliontzopoulou et al. 2012). Ecological particularities such as gigantism or cannibalism are attributed to food availability and prey selection, among other important factors (Raia & Meiri 2006, Meiri 2007). Thus, it is not accidental that dietary studies remain a hot topic in herpetology (e.g. Laverty & Dobson 2013, Rebouças et al. 2013, Brock et al. 2014) and are considered essential, especially for poorly known species (Pérez-Mellado et al. 2011).

Most lizards have adopted a generalist feeding profile (Pianka 1986, Diaz 1995). Among lacertid lizards, terrestrial invertebrates, and particularly insects, occupy a predominant part of their diet (Arnold 1987, Carretero 2004). However, the feeding ecology of the family shows an impressive plasticity and numerous factors affect the choice of prey. Widespread species often exhibit geographic variation in their diet (Carretero 2004). Lacertids' diet may also vary seasonally in response to fluctuating food availability (Pérez-Mellado et al. 1991, Díaz & Carrascal 1993). Furthermore, insular populations often deviate from the feeding preferences of their mainland kin as a result of the food scarcity prevailing on the islands (Pérez-Mellado & Corti 1993). As such, islanders tend to include more plant material in their diet (Van Damme 1999, Vervust et al. 2010) and, in some extreme cases, resort even to cannibalism (Castilla & Van Damme 1996, Pafilis et al. 2008, Pafilis et al. 2009).

The Balkan green lizard (*Lacerta trilineata* Bedriaga, 1886) is the largest species within its genus and one of the largest lacertids in Europe, second only to *Timon lepidus* (Arnold & Ovenden 2002). Snout to vent length (SVL) reaches 16 cm, tail may be twice as long and weight is around 150 g (Nettmann & Rykena 1984, Arnold 1987). The species is widespread throughout the Balkans, where it occurs in the majority of biotopes (Schmidtler 1997). In Greece, *L. trilineata* is very common both on the mainland and on several islands. Being a conspicuous species, thanks to its body size and the bright green coloration, it is the most frequently observed lizard in the Balkan Peninsula and the Greek islands (Valakos et al. 2008). Despite the aforementioned, the data on the diet of *L. trilineata* are surprisingly scarce. Contrary to other green lizards, whose feeding ecology has been adequately studied (e.g. Angelici et al. 1997, Gvoždík & Boukal 1998, Nemes 2002, Mollov et al. 2012), the only available information for *L. trilineata* comes from few old observations in one Greek and two Bulgarian populations (Werner 1903, Peters 1963, Angelov et al. 1966). Only very recently a new study provided additional data on the diet of the species, based though on a very small sample size (five specimens, Mollov & Petrova 2013).

Thanks to its wide distribution, high sexual dimorphism and differences between adults and juveniles, *L. trilineata* represents an excellent species to examine potential sexual, ontogenetic, seasonal and geographic variation in feeding ecology. In the present study, we focused on continental and insular populations from Greece and formulated four hypotheses. First, we predicted that males would have different diet composition compared to females, as consequence of their larger body size and more active foraging mode (Herrel et al. 1996, Scharf & Meiri 2013). Second, we presumed that juveniles would feed on different prey. Third, we anticipated that season would have an impact on food preferences during the year. Fourth, we expected that insular populations would demonstrate a more general diet because of the restricted food availability in the islands (Pérez-Mellado & Corti 1993, Carretero 2004).

Materials and Methods

Diet composition

To examine the prey remnants, we removed the digestive tract from 288 preserved specimens that were deposited to the Herpetological Collection of the Natural History Museum of Crete (N = 159) and the Herpetological Collection of the A. Koenig Zoological Research Institute and Museum at Bonn (N = 129). 145 of these specimens originated from the islands (12 from Lesvos, 13 from Milos, 10 from Naxos, 10 from Andros, 10 from Skiathos, 7 from Skopelos, 18 from Skyros, 65 from Crete) and 143 from mainland Greece (47 from Thessaly, 26 from Epirus, 23 from Peloponnese and 47 from Sterea Ellada, Fig. 1).

Prior to the analysis, we recorded the sex and the age (adult or juvenile) of animals and measured SVL using a digital caliper (Silverline 380244, accurate to 0.01 mm). Individuals with SVL less than 80 mm, as well as with stripes on the back and light marks on the sides were considered as juveniles (Arnold 1987, Angelici et al. 1997, Pafilis & Valakos 2008) Prey items were analysed under a binocular dissecting microscope, identified to order level whereas the number of each prey group was recorded.

We assessed the effect of season for spring, summer and autumn but not for winter, since *L. trilineata* hibernates (Nettmann & Rykena 1984, Pafilis & Valakos 2008). Plant material consumption was recorded only as frequency of presence and not as percent volume in the stomach.

Statistical analyses

We estimated the percentage of the total number of prey items found in the stomachs (%n) and also the percentage of lizards that ate a given prey taxon (F). We calculated the niche breadth (H') using the Shannon-Wiener diversity index (Krebs 1998):

$$H' = -\sum p_i \ln p_i \ ,$$

where p_i is the percentage of each prey item found in the stomachs. A t-test was performed to obtain differences of the diversity index between age classes, sexes and habitats (insular and mainland) (Zar 2010). An analysis of variance (ANOVA) with 999 permutations was used to test for differences between seasons (Gardener 2012). To further investigate the level of food specialization between mainland and island individuals (the interaction SEX × HAB) we used the Berger-Parker index (D) calculated based on the following equation (Magurran 1988):

$$D = \sum \frac{n_i \max}{N} \ ,$$

where N is the sum of the prey items in the stomach and n_i is the number of individuals from the most abundant taxon in the diet. A value closer to the unit stands for higher specialization in food preference. To generate the 95% confidence intervals between populations (HAB × SEX), we used the bootstrap re-sampling method implemented in PAST (Hammer et al. 2001).

Since the Shannon-Wiener diversity index is largely affected by the most abundant species, we also calculated the Jaccard similarity coefficient (Jaccard 1908) in order to test the differences in food composition among groups (the interaction of AGE × SEX × HAB × SEASON):

$$J_{(A,B)} = \frac{|X \cap Y|}{|X \cup Y|} \ ,$$

where X and Y correspond to the sets of entities that occur at A and B groups, respectively. In addition, we used the Pianka's overlap index (Q_{jk}) to obtain a quantitative measure of food niche similarity among groups (Pianka 1975):

$$Q_{jk} = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}} \ ,$$

where j and k refer to the two groups under comparison and p_{ij} and p_{ik} to the proportion of the food component i in each group. For the calculation of niche overlap we used the program EcoSim 7.0 (Gotelli & Entsminger 2001).

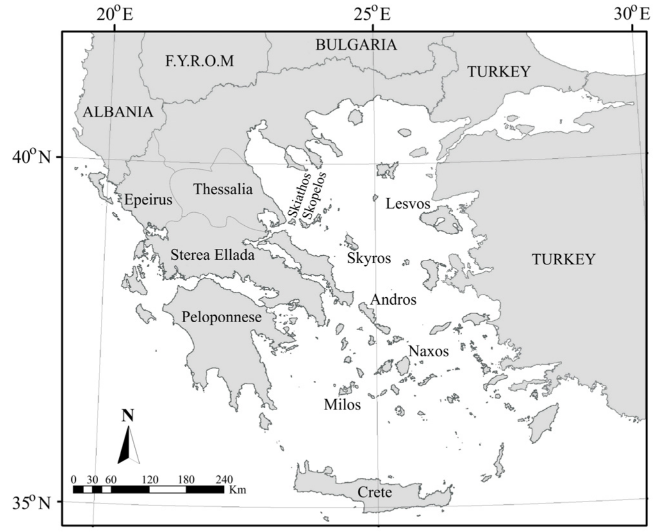

Figure 1. Map of Greece at East Mediterranean Sea, denoting the sampling localities.

Finally, chi-square test and analysis of variance (ANOVA) were used to examine the differences of plant consumption in habitats, age classes and sexes (AGE × HAB × SEX) and to test for differences between the proportion of prey items in the stomach for the interaction of AGE × HAB × SEX, while Spearman correlation was performed to examine whether F is related to %n. All statistical analyses were conducted using the computer program PAST (Hammer et al. 2001).

Results

The diet of *L. trilineata* was mainly composed of arthropods. The most predominant prey taxa throughout the year for all groups were Coleoptera, Orthoptera, Hymenoptera and Isopoda (Fig. 2), while there was a significant correlation between the proportion of the total number of prey items in the stomachs (%n) and the proportion of lizards that ate a given prey taxon (F) (Spearman test, all $r > 0.90$, all $P < 0.05$) (Table 1).

Sexual variation

Analyses revealed substantial differences regarding the taxonomic prey categories consumed by males and females (Jaccard index ~ 0.6; Supplementary material, Table S3A). In particular, we found that adult males included in their diet preys such as Diplopoda and Chilopoda, which were almost absent from female stomachs (Supplementary Material, Tables S1 and S2). However, no further differences were found between sexes either regarding their niche breadth (H') (t-test, all $P > 0.05$; see Supplementary material, Table S4) or the proportion of prey items consumed (χ^2 test, both $P > 0.05$). These results were in agreement with the high food niche overlap demonstrated by males and females coming from the same habitat (Supplementary material, Table S5). Therefore, we pooled the two sexes from each population in one group for the subsequent analysis (Table 1).

Ontogenetic variation

The comparison between adults and juveniles yielded significant differences. The latter showed a preference towards softer preys such as insect larvae, Araneae, Opiliones and Formicidae, while there was a reduction in the consumption of plant material and hard preys (such as Coleoptera and Isopoda) (χ^2 test, Fisher exact, $P < 0.05$; Supplementary material Table S6) (Table 1). These findings were also confirmed by the low values of the Jaccard index (~0.65 for islanders and ~0.45 for their mainland kin; Supplementary material, Table S3B) and the relatively low food niche overlap that was recorded between juvenile and adult lizards ($Q_{jk} < 80\%$ in most cases; Supplementary material, Table S7). The proportion of prey items in the diet of the two age classes was significantly different throughout the year (χ^2 test, $P < 0.05$; Supplementary material, Table S6). Furthermore, in the case of mainland populations, juveniles demonstrated significantly higher niche breadth than adults (Table 1 and Supplementary material, Tables S7 and S8) and lower values of the Berger-Parker index (Table 1), which indicates less specialization. Fi-

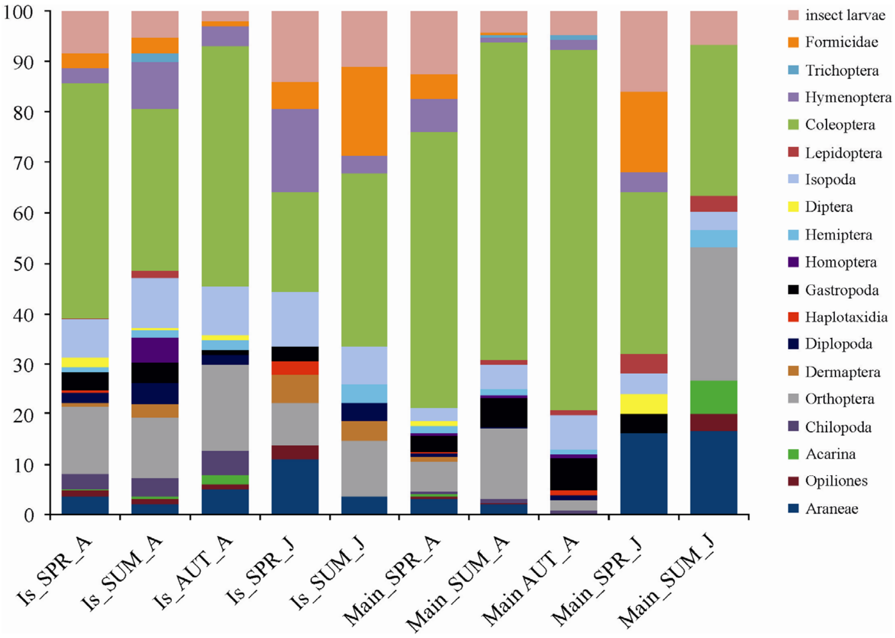

Figure 2. Proportion of prey items in the stomach (%n) for each examined population as in Table 1. Isl refers to islands; Main to mainland; A to adults; J to juveniles; SPR to spring; SUM to summer and AUT to autumn.

nally, the average number of prey items per stomach differed between adults and juveniles for all seasons examined (ANOVA, $F_{2,278} = 10.395$, $P < 0.001$; post-hoc Tukey *HSD* test), with juveniles consuming fewer prey items.

Seasonal variation

There was a clear divergence between the examined seasons (χ^2 test, Fisher exact, $P < 0.05$; Supplementary material, Table S6). Adult lizards, regardless of origin, followed the same pattern and had the lower trophic spectrum and the lower number of prey items in their stomach during autumn (ANOVA, $F_{2,278} = 10.395$, $P < 0.001$; post-hoc Tukey *HSD* test; Table 1). A high consumption of plant material was observed during spring for both types of habitat and, in this case, even for insular juveniles (χ^2 test, Fisher exact $P < 0.05$; Table 1). At the same line, we found significant differences in the proportion of prey items in the stomach (χ^2 test, Fisher exact, $P < 0.05$; Supplementary material, Table S6) and low values of the Jaccard similarity index among seasons (Supplementary material, Table S3B). The comparison of the food niche breadth during the year also revealed substantial differences, but only for adult lizards (adults: ANOVA, both $P < 0.05$ and juveniles: t-test, both $P > 0.05$; see Supplementary material, Table S8).

In the case of insular populations, adults showed the higher niche breadth values during summer (H' = 2.34), whereas no differences were revealed between spring (H' = 1.933) and autumn (H' = 1.801) (ANOVA, $F_{2,120} = 22.156$, $P < 0.05$). The opposite pattern was recorded for the Berger-Parker index (levels of specialization), where the higher values recorded during spring ($D = 0.467$) and autumn ($D = 0.475$) and lower during summer ($D = 0.319$) (Table 1). However, no differences were revealed for insular juveniles during spring and summer regarding the proportion of prey items consumed (χ^2 test, Fisher exact, $P < 0.05$; Supplementary material, Table S6) and the niche breadth (Supplementary material, Table S8), despite the low Jaccard similarity index (~0.65; Supplementary material, Table S3B). Nonetheless, despite the similar values of niche breadth of juveniles between spring and summer, the Berger-Parker index was significantly lower during spring ($D = 0.194$) compared to summer ($D = 0.444$).

On the contrary, adult lizards from the mainland showed a higher H' during spring (H' = 1.699) and lower during summer (H' = 1.199) and autumn (H' = 1.385) (ANOVA, $F_{2,120} = 5.830$, $P < 0.05$) (Table 3). The values of the Berger-Parker in-

Table 1. Diet composition of *Lacerta trilineata* from islands and mainland populations pooled for males and females (adults, A) and juveniles (J), in all examined seasons. Spring (SPR), summer (SUM) and autumn (AUT). %n refers to the percentage of prey items in the stomachs, F refers to the proportion of lizards eaten a specific prey category, H' to the Shannon-Wiener diversity index while *D* refers to Berger-Parker index.

ISLAND	SPR_A		SUM_A		AUT_A		SPR_J		SUM_J	
POPULATIONS	F	%n	F	%n	F	%n	F	%n	F	%n
Araneae	0.19	3.62	0.09	2.09	0.19	4.95	0.29	11.11	0.09	3.70
Opiliones	0.06	1.09	0.02	1.05	0.04	0.99	0.07	2.78	–	–
Acarina	0.02	0.36	0.02	0.52	0.07	1.98	–	–	–	–
Chilopoda	0.17	3.26	0.11	3.66	0.15	4.95	–	–	–	–
Orthoptera	0.44	13.04	0.38	12.04	0.41	16.83	0.21	8.33	0.27	11.11
Dermaptera	0.04	0.72	0.07	2.62	–	–	0.14	5.55	0.09	3.70
Diplopoda	0.13	2.17	0.13	4.19	0.07	1.98	–	–	0.09	3.70
Haplotaxidia	0.02	0.36	–	–	–	–	0.07	2.78	–	–
Gastropoda	0.15	3.62	0.09	4.19	0.04	0.99	0.07	2.78	–	–
Homoptera	–	–	0.09	4.71	–	–	–	–	–	–
Hemiptera	0.06	1.09	0.04	1.57	0.07	1.98	–	–	0.09	3.70
Diptera	0.04	1.81	0.02	0.52	0.04	0.99	–	–	–	–
Isopoda	0.27	7.61	0.20	9.95	0.19	9.90	0.21	11.11	0.18	7.41
Lepidoptera	0.02	0.36	0.07	1.57	–	–	–	–	–	–
Coleoptera	0.79	46.74	0.64	31.94	0.74	47.52	0.43	19.44	0.73	34.44
Hymenoptera	0.13	2.90	0.11	9.42	0.11	3.96	0.36	16.67	0.09	3.70
Trichoptera	–	–	0.07	1.57	–	–	–	–	–	–
Formicidae	0.10	2.90	0.13	3.14	0.04	0.99	0.14	5.56	0.09	17.41
Insect larvae	0.19	8.33	0.16	5.24	0.04	1.98	0.29	13.89	0.27	11.11
Plant material	0.25		0.38		0.19		0.14		0.09	
Total Preys	276		191		101		36		27	
Specimens	48		45		27		14		11	
Prey/stomach	5.75		4.24		3.74		2.57		2.45	
D	0.467		0.319		0.475		0.194		0.444	
H'	1.933		2.34		1.801		2.206		1.97	
$r_{Spearman}$	0.981		0.934		0.985		0.997		0.989	

MAINLAND	SPR_A		SUM_A		AUT_A		SPR_J		SUM_J	
POPULATIONS	F	%n	F	%n	F	%n	F	%n	F	%n
Araneae	0.15	3.08	0.09	2.05	–	–	0.27	16.00	0.33	16.67
Opiliones	0.04	0.62	0.02	0.34	–	–	–	–	0.08	3.33
Acarina	0.02	0.31	–	–	–	–	–	–	0.08	6.67
Chilopoda	0.02	0.62	0.04	0.68	0.05	0.94	–	–	–	–
Orthoptera	0.30	6.15	0.40	13.99	0.10	1.89	–	–	0.50	26.67
Dermaptera	0.07	0.92	–	–	–	–	–	–	–	–
Diplopoda	0.04	0.62	0.02	0.34	0.05	0.94	–	–	–	–
Haplotaxidia	0.02	0.31	–	–	0.05	0.94	–	–	–	–
Gastropoda	0.20	3.08	0.23	5.80	0.14	6.60	0.09	4.00	–	–
Homoptera	0.02	0.31	0.02	0.34	0.05	0.94	–	–	–	–
Hemiptera	0.11	1.54	0.04	1.37	0.05	0.94	–	–	0.08	3.33
Diptera	0.04	0.92	–	–	–	–	0.09	4.00	–	–
Isopoda	0.20	2.77	0.21	4.78	0.24	6.60	0.09	4.00	0.08	3.33
Lepidoptera	–	–	0.06	1.02	0.05	0.94	0.09	4.00	0.08	3.33
Coleoptera	0.85	54.77	0.92	63.14	0.95	71.70	0.36	32.00	0.58	30.00
Hymenoptera	0.20	6.46	0.04	1.02	0.05	1.89	0.09	4.00	–	–
Trichoptera	–	–	0.02	0.34	0.05	0.94	–	–	–	–
Formicidae	0.09	4.92	0.04	0.68	–	–	0.27	16.00	–	–
Insect larvae	0.37	12.62	0.21	4.10	0.19	4.72	0.36	16.00	0.17	6.67
Plant material	0.15		0.13		0.10		–		–	
Total Preys	325		293		106		25		30	
Specimens	46		53		21		11		12	
Prey/stomach	7.06		5.53		5.04		2.27		2.5	
D	0.548		0.717		0.632		0.32		0.30	
H'	1.699		1.199		1.385		1.888		1.827	
$r_{Spearman}$	0.96		0.989		0.979		0.996		0.992	

dex opposed to the values of the Shannon-Wiener diversity index (Table 1). Moreover, mainland juveniles showed a clear distinction in the proportion of prey taxa consumed between spring and summer (χ^2 test, Fisher exact, $P < 0.05$; Supplementary material, Table S6) and therefore low niche overlap ($Q_{jk} = 0.64$; Supplementary material, Table S7) and Jaccard similarity index (~0.34; Supplementary material, Table S3B). However, no differences were revealed in regard to niche breadth (1.888 vs. 1827) and the Berger-Parker index (0.32 vs. 0.30) between spring and summer (Table 1).

Geographical variation

Prior to any analyses, insular and mainland populations were pooled in two groups (island vs. mainland), since no significant differences were detected in the proportion of the most common prey items consumed by each single population (the two islands and the two mainland sites - χ^2 test, Fisher exact $P > 0.05$). Furthermore, Jaccard similarity index (~0.8) and niche overlap ($Q_{jk} > 0.95$) obtained high values within mainland and within insular populations.

The comparison between mainland and insular populations revealed significant differences regarding the diet composition. First, mainland lizards demonstrated a highly restricted diet, mostly composed of Coleoptera (~65%) and Orthoptera (~10%), a finding that was further confirmed by their low niche breadth. In particular, adult islanders had higher niche breadth compared to their mainland counterparts in all examined seasons (H', spring: 1.933 vs. 1.699; summer: 2.34 vs. 1.199; autumn: 1.801 vs. 1.385) (t-test, all $P < 0.05$; Table 1 and Supplementary material, Table S8). These results concurred with the higher values of the Berger-Parker index (higher specialization) in mainland lizards during all seasons (*D*, spring: 0.467 vs. 0.548; summer: 0.319 vs. 0.717; autumn: 0.475 vs. 0.631) (Table 1). We have to stress out that juveniles from the islands and mainland did not differ statistically regarding their H' (t-test, all $P > 0.05$) (Supplementary material, Table S8).

Second, we found significant differences in the proportion of prey groups in the diet of insular and mainland populations (χ^2 test, Fisher exact, $P < 0.05$; Supplementary material, Table S6). Islanders included more plant material and had lower average number of prey items per stomach compared to their mainland counterparts (χ^2 test, Fisher exact $P < 0.05$; Table 1).

Discussion

The diet of the Balkan green lizard is similar to that of the majority of large *Lacerta* and *Timon* lizards in Europe (Llorente & Pérez-Mellado 1988, Castilla et al. 1991, Hödar et al. 1996, Angelici et al. 1997, Gvoždík & Boukal 1998, Mollov et al. 2012). Our findings fell short to support the first working hypothesis: males and females shared a common pattern in their feeding ecology. The remaining three hypotheses were verified: ontogeny, season and habitat affect the feeding ecology of *L. trilineata*.

The Balkan green lizard is a generalist predator with high food niche breadth. Our results are in agreement with the study of Mollov and Petrova (2013), who recorded the presence of 13 prey categories and a low Berger-Parker index (0.33). *L. trilineata* is a widely foraging predator, feeding on numerous invertebrate taxa, both flying (Lepidoptera, Diptera, Hymenoptera, etc.) and evasive (insect larvae, Haplotaxidia, Isopoda, etc.) (Fig. 2). Coleoptera represent the predominant prey group in the diet of both adults and juveniles throughout the year, while other common prey taxa are Orthoptera, Isopoda and Hymenoptera (Table 1). An interesting finding was the low consumption of ants. Myrmecophagy is one of the most common feeding strategies among European lacertids, due to their abundance in arid environments (Pérez-Mellado et al. 1991, Pérez-Mellado & Corti 1993, Maragou et al. 1996, Valakos et al. 1997). This discrepancy should be attributed to the large body size and the subsequent high-energy requirement of *L. trilineata.* Prey size is a useful index of the food energy content (Schoener 1971, Jaeger & Barnard 1981, Díaz & Carrascal 1991) and thus a crucial factor for the choice of prey by predators (Castilla et al. 1991, Díaz & Carrascal 1991, Hödar et al. 1996). Our results suggest that *L. trilineata* avoid small size preys and prefer the richer, in terms of energy, larger arthropod taxa such as Coleoptera and Orthoptera. We have to stress out that our findings contradict previous studies supporting that ants comprise one of the main prey taxa of *L. trilineata* (Peters 1963, Angelov et al. 1966). However, these studies were based on small sample sizes (63 and 9, respectively) and thus their results have a rather weak support.

Sex had no effect on the food preferences of *L. trilineata*. In agreement with other studies, our data yielded no differences regarding the breadth of food niche between males and females (Supplementary Material, Tables S4). The high niche overlap corroborates this finding (Supplementary Material, Tables S5) (Carretero et al. 2010). This similarity should be attributed to the low variation of habitat diversity in Mediterranean ecosystems, which does not allow animals to generate significant differences in food niche breadth (Gvoždík & Boukal 1998). The only difference we detected lies in the proportion of prey taxa consumed (low Jaccard similarity index, Supplementary Material, Tables S3), with males showing a higher preference over hard preys. This finding is related to the different performance of the male feeding apparatus: males are able to bite stronger and thus have access to harder and more difficult-to-handle prey (Herrel et al. 2001, Verwaijen et al. 2002) (Supplementary Material, Tables S1 and S2).

Juveniles followed a discrete feeding pattern. Values for Jaccard index and food niche overlap (Q_{jk}) on the dietary composition of adults and juveniles were relatively low, particularly for mainland populations (Jaccard index: ~0.4 and Q_{jk}: ~0.80; Supplementary material Tables S3 and S7, respectively). These results indicate an ontogenetic shift. During their growth, lacertids undergo significant changes in the size, shape and performance of their feeding apparatus. These changes affect prey selection and, consequently, stomach content (Arnold 1993). The limited gastrointestinal capacity of juveniles and the higher bite force required for hard preys might explain the observed differences in the diet (Pough 1973, 1983, Herrel et al. 1999). These findings are in agreement with a similar study made by Peters (1963) who reported that juveniles chewed their food much better (the prey items in their stomachs were much more chopped into smaller parts) than adults.

A complementary underlying reason should be sought in the way adults exploit their environment. While adults are usually occurring in areas with dense vegetation, young lizards can be found in open meadows, with lower vegetation cover (Arnold 1987, Angelici et al. 1997). This microhabitat variation is combined with equivalent differences in arthropod availability (Vitt et al. 1997). Though similar dietary shifts are not very common in small- and medium-sized lizards (Diaz 1995), they have been frequently reported in snakes (Luiselli & Agrimi 1991, Natusch & Lyons 2012), turtles (Bouchard & Bjorndal 2006) and amphibians (Duellman & Trueb 1986, Yu et al. 2009). Ontogenetic shifts have been reported before in *L. trilineata* regarding tail autotomy performance (Pafilis & Valakos 2008). Age affects as well the diet of the species, similarly with other green lizards (Angelici et al. 1997).

In mainland populations, adults mainly fed upon Coleoptera, Isopoda, Gastropoda and Orthoptera (representing 85% of their diet). Juveniles, on the other hand, had a wider trophic spectrum and included in their diet significant proportions of soft prey taxa such as insect larvae, Araneae and Opiliones (Verwaijen et al. 2002). They also had higher food niche breadth (H') (~ 1.85 vs. 1.43) and lower levels of specialization (D) (~0.3 vs. 0.65) compared to adults (Table 1). In the case of the islanders, a striking difference emerged regarding the extent of herbivory: though adults consumed high amounts of plant material, juveniles ate considerably less (Table 1). Juveniles of large-bodied lizards show low plant consumption as consequence of their difficulty to digest plant fibres and their insufficient gut capacity and structure for supporting such a diet (Pough 1973, 1983). Moreover, juveniles need more nutritious food for their growth which is not provided by the low-energy plant material (Durtsche 2000).

Lacerta trilineata experienced seasonal variation in its diet and seems to be an opportunistic predator (Supplementary material, Tables S6 and S8). The species feeds with a wide range of prey items, based on their abundance and availability in the environment during the year. This strategy allows *L. trilineata* to cope with the strong temporal fluctuations of the arthropod diversity, which are typical of the Mediterranean ecosystems of Greece (Karamaouna 1987). We noted a continuous decrease in the mean number of prey items per stomach from spring to autumn (Table 1). However, the mean number of prey items lies within the range known for other green lizards (Angelici et al. 1997, Gvoždík & Boukal 1998, Mollov et al. 2012).

Arthropod populations on Mediterranean islands decrease dramatically during summer as consequence of drought, leaving few prey choices to lizards (Carretero 2004, Pafilis et al. 2009, Pafilis et al. 2013). As a result, the available alternatives are greatly exploited (Pérez-Mellado & Corti 1993, Hödar et al. 1996). The observed higher summer percentages of Hemiptera, Formicidae and Homoptera in the insular populations of *L. trilineata* reflects this strategy, which is further favoured by the increased abundance of these insect groups in the Aegean islands during summer (Paraschi 1988). On the other hand, the limited presence of

Coleoptera and insect larvae at the same season should be attributed to their reduced activity and densities during summer (Karamaouna 1987, Trihas & Legakis 1991). Similar seasonal shifts in the consumed prey have been reported from other Mediterranean lacertids (Valakos 1986, Pérez-Mellado & Corti 1993, Adamopoulou et al. 1999).

The diet of island lizards remained rather stable throughout the year. As a result, the niche breadth remained constantly high (Table 1). These findings are in agreement with the foraging theory, which predicts that a decrease in food abundance will lead to a lower food specialisation (Schoener 1971, Stephens & Krebs 1986) and thus a higher niche breadth (Table 1). Plant consumption represents a deviation in this stable pattern. Islanders ate more plant material during summer, most probably due to the temporary food-scarcity of the environment (Pérez-Mellado & Corti 1993, Cooper & Vitt 2002 and references therein).

Mainland populations showed a different pattern regarding the niche breadth. In this case, the higher values were observed during spring and not summer. During this season the diet of mainland *L. trilineata* consisted of 17 taxonomic prey categories with Coleoptera and insect larvae representing 67% of the diet (Table 1). An unexpected finding was the high specialization during summer and autumn, with a diet that consisted almost exclusively of only 5 prey categories (Coleoptera, Orthoptera, Gastropoda, Isopoda and insect larvae) that covered approximately 85% of the total diet composition. The food niche breadth for summer and autumn were similar (Table 1), mainly because of the large consumption of Coleoptera and considerably lower compared to the summer one.

Habitat type had a clear effect on the diet of *L. trilineata*. Our data suggested significant dietary differences between island and mainland populations that are probably associated with particular features (e.g. low food availability) (Carretero 2004, McConnachie & Alexander 2004, Carretero et al. 2010). The most striking difference was the higher consumption of plant material by the island populations (~30%) compared to the mainland ones (~10%). The high proportion of plant material suggests that herbivory is a common practice and plants are not accidentally consumed by islanders. Though plant consumption is fairly common in insular lacertids (Pérez-Mellado 1989, Pérez-Mellado & Corti 1993, Van Damme 1999, Cooper & Vitt 2002, Lo Cascio et al. 2006), green lizards are not considered regular plant eaters. Even when plant material was discovered in their stomachs, the percentage was very low (less than 10%, Gvoždík & Boukal 1998).

The food scarcity at the Aegean islands was reflected in the lower mean number of prey items per stomach in the insular populations (Table 1). The limited food resources force islanders to broaden their trophic spectrum. As a result, islanders had a higher food niche breadth (H') and displayed lower selectivity (*D*) for all examined seasons (Table 1). Mainland populations included in their diet lower proportions of Orthoptera and Isopoda, while taxa such as Dermaptera, Diplopoda and Chilopoda were almost completely absent from their diet (Fig. 2). However, these differences were not clearly represented in the food niche overlap (>90%; Supplementary material, Table S7) probably due to the extremely high proportion of Coleoptera.

Even though relatively "new" disciplines provide valuable information, "traditional" research branches, such as feeding ecology, still have important information to yield, especially when combined with a solid phylogenetic basis (Hurston et al. 2009). In the case of *L. trilineata*, though the phylogeny and physiology of the species have been satisfactory assessed (Godinho et al. 2005, Pafilis & Valakos 2008, Ahmadzadeh et al. 2013a, Ahmadzadeh et al. 2013b, Sagonas et al. 2013, Sagonas et al. 2014), detailed studies of diet were still lacking. We believe that new data on reptilian diet may shed light to an array of physiological, anatomical and ecological adaptations at the population level.

Acknowledgments. We thank Prof. Dr. W. Boehme, who kindly allowed us to examine the *L. trilineata* specimens of the Zoologisches Forschungsmuseum Alexander Koenig, or Zoological Research Museum A. Koenig. We express our gratitude to three anonymous reviewers for providing comments that significantly improved an earlier version of the manuscript.

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