ISRAEL JOURNAL OF ZOOLOGY, Vol. 48, 2002, pp. 207–219

DIET OF A LACERTID LIZARD (*PODARCIS MILENSIS*) IN AN INSULAR DUNE ECOSYSTEM

Chloe Adamopoulou* and Anastasios Legakis
Zoological Museum, Department of Biology, University of Athens,
Panepistimioupolis GR-157 84, Greece

ABSTRACT

This study reports on the seasonal, sex, and age differences in the diet composition of a population of the lacertid lizard *Podarcis milensis* inhabiting an arid sand dune on Milos Island (Aegean Archipelago, Greece). Stomach contents of 191 animals were analyzed and compared with prey availability data. The most important prey types were Hemiptera, Coleoptera (other than Tenebrionidae), spiders, and ants. Other prey items included plant material and insect larvae, both constantly consumed throughout the year. Differences in the taxonomic composition of the diet were found between males and females and between juveniles and all other classes. The greatest similarity of diet composition between the sexes and ages examined was during summer. The foraging patterns observed are discussed within the context of the specific study system: an insular, low productivity, sand dune ecosystem.

INTRODUCTION

The feeding ecology of lacertid lizards has received considerable attention in the last decade. Numerous studies have been published, mostly describing the diet of lizards inhabiting the Western Mediterranean (e.g., Pollo and Pérez-Mellado, 1988; Castilla et al., 1991; Carretero and Llorente, 1993; Pérez-Mellado and Corti, 1993), but some also for the Eastern Mediterranean (Valakos, 1986; Chondropoulos et al., 1993). Here, we report data on the diet of *Podarcis milensis,* a small endemic lacertid that is found in the Aegean Archipelago, Greece. The species is restricted to the Milos islands group (Milos, Kimolos, Polyaigos, Antimilos) and the islets Velopoula, Ananes, and Falkonera.

Our aim was (1) to describe the diet of this species; (2) to examine food selection patterns in relation to prey availability; and (3) to discuss the results in a broader context, that is, the way foraging decisions are shaped by a small insectivorous lizard inhabiting a low productivity environment.

---

*Author to whom correspondence should be addressed. E-mails: cadam@biol.uoa.gr; alegakis@biol.uoa.gr

[redacted]

MATERIALS AND METHODS

STUDY ANIMAL

P. milensis is a small (adult SVL: 42–70 mm) heliothermic lizard that occurs in a wide variety of habitats ranging from stone walls and cultivated fields to the beach shore. Males are larger and more brightly colored than females (Arnold and Burton, 1978). *P. milensis* has no real lizard competitors, as it is the only small lacertid in the area. The population under study is active year-round and is characterized by a long breeding season. Clutch size is exceptionally small, ranging from 1 to 3 eggs (Adamopoulou and Valakos, 2000).

STUDY AREA

The study area is situated in the center of Milos Island between Lake Achivadolimni and the beach. It is an arid, sandy, back-dune ecosystem that is exposed to high daily temperatures and offers a habitat low in structural diversity. Fifty-two percent of the study plot (plot dimensions 70 × 30 m) is covered by vegetation, while the rest is an open area of bare sand. Vegetation consists mainly of *Juniperus oxycedrus* ssp. *macrocarpa* (62.23% of the study plot—but only three individuals in it) and *Coridothymus capitatus* (22.54%, more than 100 ind.) (Adamopoulou, 1999). Lizards are found under or near *C. capitatus* and are rarely seen on bare sand.

PREY AVAILABILITY

Prey availability was estimated using the pitfall trapping method, which is widely used by herpetologists since it consists of an easy and secure way of estimating the available invertebrate prey in the environment (Díaz, 1995). In total, 20 pitfall traps (small plastic vessels buried up to their rims in the soil, containing ethylene glycol solution 5 cm in height) were placed within the habitat of *P. milensis* covering all the potential microhabitats (bare sand/under *Juniperus* bush/ under *Coridothymus* bush) for a total of 12 months and were emptied every month.

DIETARY ANALYSIS

All specimens used for the dietary analysis came from the pitfall traps used for the estimation of food availability. Due to their small size, lizards, once in the trap, could not get out. The lizards died soon after falling into the trap, and therefore it is expected that digestion would be arrested, leaving chitinous parts of arthropods and cellulose from plant material (leaves and seeds) unaffected. As a result, we were provided with a monthly sample of all sexes and ages. After collection, specimens were injected with formalin and then transferred to 70% ethanol. For each lizard, the SVL was measured to the nearest 0.1 mm, and the entire digestive tract was removed and examined for the presence of prey remnants. All specimens were deposited in the herpetological collection of the Zoological Museum of the University of Athens.

For the dietary analyses, *P. milensis* were divided into age classes as follows: adult males SVL $\geq$ 47 mm, adult females SVL $\geq$ 42 mm, subadults SVL $<$ 42 or 47 mm (according to sex), and juveniles SVL < 35 mm (Adamopoulou, 1999). Prey items were identified to family or order level. Whole individual prey items were measured for body length and width under a stereoscope to the nearest 0.01 mm (L: mean body length, L_{max}: maximum body length, W: mean body width, and W_{max}: maximum body width). The contribution of each prey type in the diet was quantified by calculating two indices: relative abundance (percentage of total prey types corresponding to a specific prey type—%n) and relative incidence (percentage of stomachs containing the specific prey type—F). Prey length was grouped in 11 classes (1 mm intervals). Niche breadth was calculated with the Shannon–Wiener index (H′) (standardized formula). Overlap in the diet between sexes and ages was estimated using the symmetric index of Pianka (1973), while electivity was calculated with Ivlev's index (1961). Correlation between prey availability and stomach contents was estimated using Spearman rank correlations. Finally, wherever needed, data were transformed (either with log or with square root) before the application of the appropriate statistical test.

In the beginning of the analysis, we used the G-test in monthly stomach and trap data to check for differences between months. The months of each set of data were pooled together into the following seasons: summer = June–September, fall = October–December, winter = January–March, and spring = April–May (no significant difference within each season, $p > 0.05$). For other statistical analysis, ANOVA, ANCOVA, and G-test were used.

RESULTS

TAXONOMIC COMPOSITION OF THE DIET

In total, the diet of 191 lizards was examined (41 males, 79 females, 48 subadults, and 23 juveniles). 1467 prey items were identified. Lizards preyed mainly on ants, Hemiptera, Coleoptera, Araneae, and insect larvae. With respect to relative incidence, Hemiptera, Coleoptera, Araneae, and ants were the dominant groups in the diet (Table 1). There was a significant positive correlation between relative abundance and relative incidence of prey groups for all lizard classes (Table 1, $r_s = 0.98$, $p < 0.0001$). Hence, groups that present the highest percentages in the stomachs were also the most frequently eaten prey. The taxonomic composition of the diet of males differed from that of females ($G = 32.52$, $df = 21$, $p < 0.05$). Males seemed to have a broader diet, frequently consuming groups such as Pseudoscorpiones, Orthoptera, and Hymenoptera (other than ants). Subadults preyed on the same groups that males and females did ($G = 18.46$, $df = 18$ and $G = 21.58$, $df = 20$, respectively, for both $p > 0.05$). Juveniles differed from all the other classes (for all $p < 0.05$) with respect to the taxonomic composition of their diet, which is the narrowest. For the Coleoptera identified in the diet of all lizards, these were: Curculionidae (47.83%), Carabidae (32.61%), and Tenebrionidae (15.22%).

SEASONAL VARIATION IN DIET COMPOSITION

Males differed from females in the taxonomic composition of their diet during all seasons except summer (Table 2). The estimates of dietary overlap indicate that the

Table 1

Relative abundance (%n) and relative incidence (F) of the various prey groups in the diet of the lizard *P. milensis* according to sex and age

Prey group	Males		Females		Subadults		Juveniles		Total (m+fem+sub+juv)	
	%n	F	%n	F	%n	F	%n	F	%n	F
Gastropoda	4.20	21.95	8.35	38.46	0.00	0.00	2.86	14.58	5.21	24.34
Opilionida	2.10	14.63	0.77	6.41	1.09	4.35	0.57	4.17	1.03	7.41
Araneae	8.04	51.22	7.88	50.00	2.17	17.39	7.71	43.75	7.13	44.44
Pseudoscorpiones	1.05	7.32	0.15	1.28	0.00	0.00	0.00	0.00	0.27	2.12
Acarina	2.10	9.76	1.08	3.85	1.09	8.70	0.57	4.17	1.17	5.82
Isopoda	0.35	2.44	0.46	2.56	0.00	0.00	0.00	0.00	0.27	1.59
Amphipoda	1.05	2.44	0.31	2.56	0.00	0.00	0.29	2.08	0.41	2.12
Chilopoda	0.35	2.44	0.31	2.56	0.00	0.00	0.57	2.08	0.34	2.12
Collembola	1.40	7.32	0.93	6.41	2.17	8.70	2.29	12.50	1.51	8.47
Dyctioptera	0.00	0.00	0.31	2.56	0.00	0.00	0.00	0.00	0.14	1.06
Orthoptera	2.45	17.07	0.15	1.28	0.00	0.00	0.57	4.17	0.62	4.76
Hemiptera	27.62	73.17	18.24	66.67	29.89	82.61	31.71	77.08	24.67	72.49
Hymenoptera	7.34	43.90	5.41	26.92	3.80	30.43	4.57	31.25	5.35	31.75
Ants	14.34	29.27	25.5	33.33	49.46	43.48	21.43	39.58	25.5	35.45
Isoptera	0.00	0.00	0.15	1.28	0.00	0.00	0.00	0.00	0.07	0.53
Lepidoptera	0.35	2.44	0.15	1.28	0.00	0.00	0.00	0.00	0.14	1.06
Diptera	3.15	14.63	6.49	21.79	2.72	17.39	3.71	22.92	4.73	20.11
Coleoptera	13.29	58.54	14.37	61.54	3.26	21.74	16.00	60.42	13.23	56.08
Insect larvae	7.34	34.15	5.56	26.92	2.72	17.39	5.14	27.08	5.41	26.98
Seeds	1.05	4.88	1.70	8.97	0.00	0.00	0.86	4.17	1.17	5.82
Other plant mat.	1.40	9.76	0.77	6.41	1.09	8.70	0.29	2.08	0.82	6.35
Cannibalism	0.35	2.44	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.53
Undetermined	0.00	0.00	1.08	7.69	0.54	4.35	0.86	2.08	0.75	4.23
No. of prey items	286		647		350		184		1467	
No. of lizards ex.	41		79		48		23		191	
Shannon–Wiener index (H′)	0.78		0.72		0.72		0.61		0.69	
r_s	$r_s = 0.96$, $p < 0.0001$		$r_s = 0.97$ $p < 0.0001$		$r_s = 0.97$ $p < 0.0001$		$r_s = 0.95$ $p < 0.0001$		$r_s = 0.98$ $p < 0.0001$	

Table 2

Comparison of the taxonomic composition of the diet between each age and sex class according to %n (G test, *: statistically significant value, –: no sample) and seasonal variation of the dietary overlap index (Q) of Pianka (1973) for all age and sex classes of *P. milensis*

Age and Sex	Summer		Fall		Winter		Spring	
	G-test	Q	G-test	Q	G-test	Q	G-test	Q
Males/females	$p > 0.5$	0.94	$p < 0.05$*	0.91	$p < 0.05$*	0.88	$p < 0.05$*	0.71
Subadults/juveniles	$p < 0.05$*	0.91	$p < 0.05$*	0.77	–	–	–	–
Subadults/males	$p > 0.5$	0.99	$p < 0.05$*	0.84	$p > 0.5$	0.98	–	–
Subadults/females	$p > 0.5$	0.96	$p < 0.05$*	0.89	$p > 0.5$	0.89	–	–

greatest similarity of diet composition between each compared pair is during summer (Table 2). The opposite is true for the diet of the adults in spring. Additionally, an ANOVA was performed on the relative incidence of the major prey groups (Araneae, Hemiptera, Coleoptera, Ants, seeds, and insect larvae) (data square-root-transformed) between the seasons. Lizards consumed Hemiptera, ants, seeds, and insect larvae throughout the year (Table 3). However, the same was not true for Coleoptera and spiders: both were consumed less during summer. When using only the two sexes, we found a significant seasonal variation of Hemiptera in the male diet (Table 3). It must be noted that the availability of all the above-examined prey groups in the pitfall traps showed a seasonal variation, fluctuating dramatically throughout the year (ANOVA on data square-root-transformed; for all arthropods $p < 0.001$, Adamopoulou, 1999).

PREY SIZE

The size distribution of the four major prey groups encountered in the stomachs of *P. milensis* is presented in Fig. 1. In three of the four cases, size distribution was skewed towards the smaller length classes. In fact: (1) almost 70% of the ants consumed belong

Table 3

Analysis of variance between the seasons of the relative incidence of major prey groups in the diet of *P. milensis*. *: statistically significant value, min/max: the seasons during which minimum and maximum values were found, respectively

Prey type	Males	Females	Total (m+f+sub+juv)
Araneae	0.23	0.87	0.04* min:summer/max:spring
Hemiptera	0.005* min:fall/max:summer	0.76	0.26
Coleoptera	0.9	0.42	0.006* min:summer/max:spring
Ants	0.63	0.54	0.07
Insect larvae	0.35	0.66	0.6
Seeds	0.55	0.24	0.08

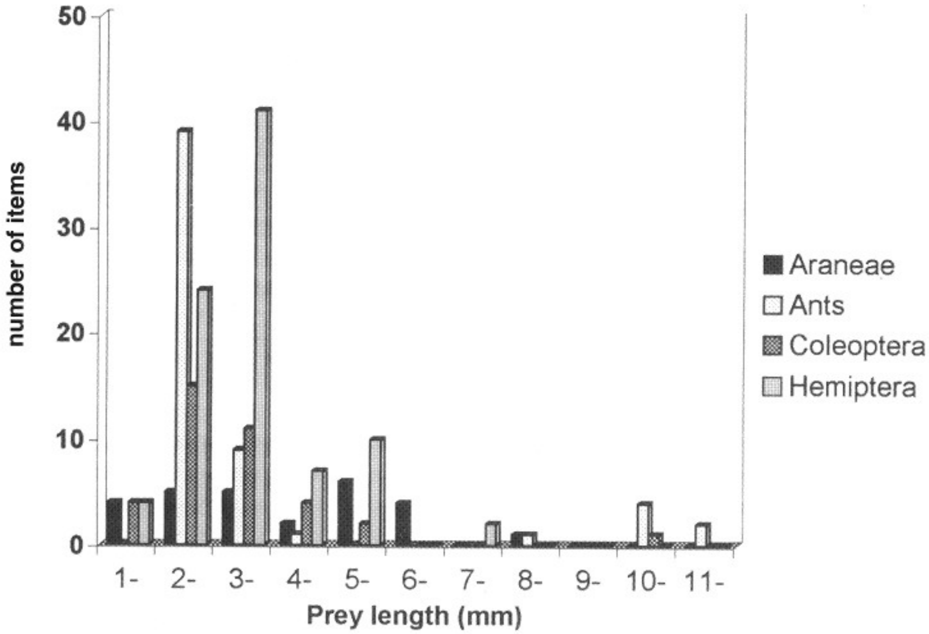

Fig. 1. Distribution of the length (in classes of 1 mm) of the items of four major prey groups encountered in the diet of *P. milensis*.

to the length class of 2 mm, (2) the majority (more than 80%) of both Hemiptera and Coleoptera are smaller than 4 mm, and (3) spiders are the only prey group that shows a wide range of lengths in the diet (skewness analysis: ants = 3.01, Coleoptera = 1.68, Hemiptera = 2.01, and Araneae = 0.2).

In addition, there was no statistically significant difference between the seasons regarding the examined prey sizes found in the diet (ANOVA, log-transformed data for all ages and sexes, L: $F_{3,91} = 2.15$, L_{max}: $F_{3,91} = 1.49$, W: $F_{3,83} = 1.46$, W_{max}: $F_{3,83} = 1.94$, all $p > 0.05$). Restricting the analysis to adults only, the results were the same (for all $p > 0.05$). Hence, lizards preyed on the same range of sizes during the course of the season. Significant differences were found in the size of the prey items eaten by lizards of different age and sex classes: males consume prey items of larger length (L and L_{max}) and width (W and W_{max}) than those consumed by females (ANOVA of log-transformed data, L: $F_{4,90} = 6.56$, L_{max}: $F_{4,90} = 4.34$, W: $F_{4,82} = 3.27$, W_{max}: $F_{4,82} = 4.88$, all $p < 0.05$). When controlled for body size, this difference fell away (ANCOVA of log-transformed data, (SVL) as a covariate, L: $F_{4,89} = 1.59$, L_{max}: $F_{4,89} = 1.62$, W: $F_{4,81} = 0.77$, W_{max}: $F_{4,81} = 1.9$, all $p > 0.05$). Overall diet overlap regarding the size of the prey consumed by each sex was low: Q = 0.5 (for each season as follows: summer: Q = 0.88, fall: Q = 0.46, winter: Q = 0.68, and spring: Q = 0.58).

FOOD AVAILABILITY AND ELECTIVITY

Seasonal variation of the relative abundance of the five most important prey groups in the traps and in the diet of adult lizards is presented together with electivity scores in Table 4. According to these results, Hemiptera, ants, and insect larvae were selected during all seasons and by both sexes (high positive electivity scores). Coleoptera seemed to be avoided by both sexes during all times of the year (negative electivity scores). The relative abundance of the five prey groups in the diet (r) in four out of the five examined cases showed a non-significant negative correlation with their abundance in the traps (p) (Table 5). Hence, there was no indication that the proportion of a prey type in the diet increased as the relative abundance of that type increased in the environment. Only for ants did we find a positive significant correlation with the male diet.

Table 4

Seasonal variation of the relative abundance for five important prey groups in the diet of the lizard *P. milensis*, relative abundance in the traps, and electivities of male and female lizards

Prey group	Summer		Fall		Winter		Spring	
	Males	Females	Males	Females	Males	Females	Males	Females
Araneae								
Diet (%n)	5.75	6.57	9.09	8.02	5.88	7.53	10.98	8.70
Traps (%n)	7.60		4.92		4.56		1.30	
Electivity (E)	–0.14	–0.07	0.30	0.24	0.13	0.25	0.79	0.74
Hemiptera								
Diet (%n)	24.14	14.6	11.36	20.32	44.12	24.73	25.61	16.09
Traps (%n)	0.95		6.76		5.97		0.55	
Electivity (E)	0.92	0.88	0.25	0.50	0.76	0.61	0.96	0.93
Ants								
Diet (%n)	29.89	43.07	13.64	13.90	5.88	11.83	6.10	30.00
Traps (%n)	4.84		2.82		1.73		1.79	
Electivity (E)	0.72	0.80	0.66	0.66	0.55	0.74	0.55	0.89
Coleoptera								
Diet (%n)	12.64	12.41	20.45	14.97	10.29	15.05	15.85	14.78
Traps (%n)	48.96		25.31		27.36		84.34	
Electivity (E)	–0.59	–0.70	–0.11	–0.29	–0.45	–0.26	–0.68	–0.60
Insect larvae								
Diet (%n)	5.75	5.11	6.82	5.35	7.35	4.30	8.54	6.52
Traps (%n)	0.44		0.67		1.34		0.18	
Electivity (E)	0.86	0.84	0.82	0.78	0.69	0.53	0.96	0.95

Table 5

Spearman rank correlation between relative abundance of the prey groups in the diet (r) and in the traps (p). r_s: Spearman correlation coefficient, *: Statistically significant value

Prey group	r_s (p vs. r)		
	Males	Females	Total $_{(m+f+sub+juv)}$
Araneae	–0.8	–0.8	–1*
Hemiptera	–0.4	0.6	0.8
Ants	1 *	0.8	0.8
Coleoptera	–0.2	–0.6	–0.4
Insect larvae	–0.2	–0.8	–0.2

DISCUSSION

The results suggest that *P. milensis* feeds mainly on arthropods, as do the majority of lacertid lizards (e.g., Pérez-Mellado, 1982; Arnold, 1987; Carretero and Llorente, 1993; Gil et al., 1993; Carretero et al., 2001).

Diet composition was found to vary according to sex and season; nevertheless, differences were not so pronounced (e.g., niche breadth was not that different between adults). The greatest niche overlap between the two sexes and age classes (regarding both diet composition and prey size) was observed during summer (also the largest value of the Pianka overlap index, both for the diet composition and the prey size). In the Mediterranean ecosystems, summer is the period of low food availability (Di Castri and Vitali-Di Castri, 1981), lizards are thus expected to converge in their trophic preferences. Indeed, in the sand dune of Achivadolimni, the arthropod community showed the smallest values of diversity during summer (Adamopoulou, 1999). However, probably the most interesting point emerging from this study is that the examined population shows several specialized patterns of foraging activity, such as myrmecophagy, preference for clumped prey, consumption of plants and of unusual prey groups (such as Amphipoda), and cannibalism. These patterns have been reported from other insular populations of the genus *Podarcis,* and may be caused by factors commonly acting on these populations.

Myrmecophagy is often encountered in the insular populations of the genus *Podarcis* (Ouboter, 1981; Quayle, 1983; Pérez-Mellado and Corti, 1993) or in populations that inhabit arid areas (Pianka, 1971; Robson and Lambert, 1980), as it represents an optimum strategy in arid environments (Pianka, 1986). However, in sandy areas ants are usually rare due to the special physical characteristics of the substratum (Cloudsley-Thompson, 1984). We do not know if lizards actually search for them or they just eat them when they find them. Ants are small, quite chitinized, and they often contain toxic compounds. Their "handling" cost is expected to be fairly large (Díaz and Carrascal, 1993). Yet, this high cost is compensated by the low amount of energy spent by the lizard in its effort to pursue the prey, due to its aggregated spatial distribution (Pianka, 1993). Eventually, the consumption of ants is economically profitable for the lizard in certain environments (Pollo and Pérez-Mellado, 1988, 1991). Likewise, the consumption of clumped prey in general (such as of ants and Hemiptera) evokes less predation risks for the lizard (Pérez-Mellado, 1992; Gil et al., 1993).

Lizards seem to avoid Coleoptera despite their abundance in the sand dune area. The majority of them (as indicated by the prey availability data) belong to the family Tenebrionidae (93%, Adamopoulou, 1999). This family is well represented in the Mediterranean basin, especially in arid and sandy ecosystems (Ghabbour and Shakir, 1980; Falacci et al., 1994) and it is characterized by a strongly chitinized exoskeleton (Colombini et al., 1994). Lizards, on the other hand, seem to prefer prey of the family Curculionidae (47.82% in the diet vs. 0.05% in the traps, Adamopoulou, 1999). Instead, only the 15% (93% in the traps) of the consumed Coleoptera belong to the family of Tenebrionidae, suggesting that lizards actually avoid them, probably because they need to spend a lot of energy to crush their exoskeleton. Grimmond et al. (1994) have found that *Chalcides* requires 50% more energy in order to crush and swallow the heavy exoskeleton of a beetle than to eat a soft-bodied insect larva.

Moreover, the animals show a steady preference for insect larvae. Pollo and Pérez-Mellado (1988) argue that this choice could be based on the larva's low content in chitin, large body size, and low capacity to move. Alternatively, this preference may be related to their high water content (Adamopoulou et al., 1999), which exceeds 50% (Roots, 1978). For example, insect larvae are absent from the diet of *P. peloponnesiaca* that is found in the much wetter conditions of the Peloponnese, S. Greece (Maragou et al., 1996).

Plant parts were eaten regularly throughout the year, which most likely excludes their accidental swallowing. Seeds are rich in water and nutritional content and represent a directly available source of energy (Golley, 1961). Pough (1973) suggested that herbivory is profitable only to large-bodied (>100 g) species of lizards. However, recent studies have shown that herbivory is in fact quite significant in the diet of small Mediterranean lacertids that are distributed in islands or isolated areas with low food availability at least during a particular season of the year (Sadek, 1981; Sorci, 1990; Lunn, 1991; Pérez-Mellado et al., 2000). Van Damme (1999), reviewing the diet of 97 populations of lacertid lizards, found an association between herbivory and insularity. He stated two possible explanations for the observed tendency: (a) poor arthropod faunas and (b) low predation pressure in the island conditions. While the first is true for the sand dune environment of Achivadolimni (Adamopoulou, 1999), the second does not seem very plausible. *P. milensis* suffers quite high predation pressure that is similar to the conditions encountered by mainland lizard species (Pérez-Mellado et al., 1997; Adamopoulou, 1999). Other *Podarcis* populations, such as those of the endemic insular species of the Balearics, *P. lilfordi*, consume plant material only during summer (Pérez-Mellado and Corti, 1993). In contrast, *P. milensis* consumes plant material all year round, a fact implying that other factors could be involved in this choice—potentially the demand for a nutritionally balanced diet (Pulliam, 1975; Rapport, 1980).

The data support the consumption of groups that show an aggregated distribution—

also mirrored by the narrow range of prey sizes found in the diet. However, whether this is the result of active choice or pure opportunism is still unclear. Males, for instance, due to their larger size (having larger heads than females, Adamopoulou, 1999) are capable of exploiting a wider range of prey sizes. Yet they usually prey on ants, Hemiptera, and Curculionidae (which constitute a concentrated food supply) and occasionally on groups that show a seasonal distribution in the environment (e.g., Orthoptera). By feeding on small clumped prey, animals can meet their energy requirements in the shortest possible time and consequently devote the rest of their available time elsewhere (e.g., reproduction, Adamopoulou and Valakos, 2000). Spiders were the only group examined showing a wider size distribution in the diet. This could be due to their physical characteristics. Díaz and Carrascal (1993), while testing the prey choice of the lizard *Psammodromus algirus,* concluded that soft and rounded arthropods (like Hemiptera and Araneae) seemed to be a more profitable prey than the harder and elongated ones (such as Coleoptera and ants). This may be due to the "handling" cost of each prey type (determined as the time between capturing and swallowing the prey), predicted by particular characteristics such as the degree of chitinization (Díaz and Carrascal, 1993). Hemiptera were found to be the most profitable prey items having a faster handling time.

In sandy environments, discontinuity in vegetation coverage produces a mosaic of microhabitats for the arthropods (and other ectotherms): Bush patches offer shade, organic material, and protection from the environmental extremes, while bare sand has the opposite characteristics (Wallwork, 1976). In our study plot, the sites of high trophic availability (situated at the base of *C. capitatus* bushes) were very well defined, and they alternated with equally well defined sites of bare sand (low and/or no food availability). Lizards spent most of their time in these food "islands", which at the same time constitute the best sites for thermoregulatory purposes as well as for predator avoidance (Adamopoulou, 1999). Similar foraging behavior has been noted in other populations of Lacertidae that inhabit arid open areas, such as the genus *Acanthodactylus* in Morocco (Pérez-Mellado, 1992), in other lacertids such as the genus *Meroles* in South Africa (Cooper and Whiting, 1999), as well as in members of other families (*Cnemidophorus tigris*, Anderson, 1993; *Uma inornata*, Durtsche, 1995). Considering all the above, we suggest that foraging is traded-off against other activities, such as social and/or reproductive behavior or predator avoidance, which could constrain and eventually rule foraging decisions, namely, effort and, especially, time spent on the acquisition of food. Utilizing clumped resources thus solves two problems: the time-related ones (e.g., less predation risk), and the exploitation of a low productivity environment in an optimal way.

ACKNOWLEDGMENTS

Part of this work was financed by the Hellenic General Secretariat for Research and Technology (Project PENED 95, 95ED2.3-1298). All specimens were collected according to the provisions set by the Presidential Decree 67/81. We would like to thank all the field crew of Milos Island.

REFERENCES

Adamopoulou, C. 1999. Structure and function of epigeic animal communities with emphasis in the lizard *Podarcis milensis* (Sauria: Lacertidae), in insular ecosystems of the Aegean. Ph.D. thesis, Univ. of Athens.

Adamopoulou, C., Valakos, E.D. 2000. Small clutch size in a Mediterranean endemic lacertid *(P. milensis)*. Copeia 2000 (2): 610–614.

Adamopoulou, C., Valakos, E.D., Pafilis, P. 1999. Summer diet of *Podarcis milensis*, *P. gaigeae* and *P. erhardii* (Sauria: Lacertidae). Bonn. Zool. Beitr. 48 (3–4): 275–282.

Anderson, R.A. 1993. Analysis of foraging in a lizard, *Cnemidophorus tigris*: Salient features and environmental effects. In: Wright, J.W., Vitt, L.J., eds. Biology of whiptail lizards (Genus *Cnemidophorus).* Oklahoma Museum of Natural History, Norman, Oklahoma, pp. 83–116.

Arnold, E.N. 1987. Resource partitioning among lacertid lizards in southern Europe. J. Zool. (B) 1: 739–782.

Arnold, E.N., Burton, J.A. 1978. A field guide to the reptiles and amphibians of Britain and Europe. Collins, London, 272 pp.

Carretero, M.A., Llorente, G.A. 1993. Feeding of two sympatric lacertids in a sandy coastal area (Ebro Delta, Spain). In: Valakos, E.D., Boehme, W., Pérez-Mellado, V., Maragou, P., eds. Lacertids of the Mediterranean region. Hellenic Zool. Soc., pp. 155–172.

Carretero, M.A., Llorente, G.A., Santos, X., Montori, A. 2001. The diet of an introduced population of *Podarcis pityusensis*. Is herbivory fixed? In: Vicente, E., Crespo, E.G., eds. Mediterranean Basin lacertid lizards—a biological approach. Proc. 2nd Int. Symp. on the lacertids of the Mediterranean Basin. Faro, Algarve, Portugal, April 1995. Instituto da Conservação da Natureza, Portugal, pp. 113–124.

Castilla, A.M., Bauwens, D., Llorente, G.A. 1991. Diet composition of the lizard *Lacerta lepida* in central Spain. J. Herpetol. 25: 30–36.

Chondropoulos, B.P., Maragou, P., Valakos, E.D. 1993. Food consumption of *Podarcis taurica ionica* (Lehrs, 1902) in the Ionian islands (Greece). In: Valakos, E.D., Boehme, W., Pérez-Mellado, V., Maragou, P., eds. Lacertids of the Mediterranean region. Hellenic Zool. Soc., pp. 173–182.

Cloudsley-Thompson, J.L. 1984. Introduction. In: Cloudsley-Thompson, J.L., ed. Key environments: Sahara Desert,. Oxford, Pergamon Press, pp. 1–15.

Colombini, I., Chelazzi, L., Falacci, M., Palesse, L. 1994. Zonation and surface activity of some Tenebrionid beetles living on a mediterranean sand beach. J. Arid Environ. 28: 215–230.

Cooper, W.E.Jr., Whiting, M.J. 1999. Foraging modes in lacertid lizards from southern Africa. Amphibia-Reptilia 20: 299–311.

Díaz, J.A. 1995. Prey selection by lacertid lizards: a short review. Herpetol. J. 5: 245–251.

Díaz, J.A., Carrascal, L.M. 1993. Variation in the effect of profitability on prey size selection by the lacertid lizard *Psammodromus algirus*. Oecologia (Berlin) 94: 23–29.

Di Castri, F., Vitali-Di Castri, V. 1981. Soil fauna of Mediterranean-climate regions. In: Di Castri, F., Goodall, D., Specht, R.L., eds. Ecosystems of the World 11, Mediterranean-type shrublands, Elsevier Scientific Publishing Company, New York, pp. 445–478.

Durtsche, R.D. 1995. Foraging ecology of the fringe-toed lizard, *Uma inornata*, during periods of high and low food abundance. Copeia 1995: 915–926.

Falacci, M., Colombini, I., Chelazzi, L. 1994. An analysis of the Coleoptera living along a Tyrrhenian beach-dune system: abundances, zonation and ecological indices. Vie Milieu 44 (3/4): 243–256.

Ghabbour, S.I., Shakir, S.H. 1980. Ecology of soil fauna of mediterranean desert ecosystems in Egypt: III. Analysis of *Thymelaea* mesofauna populations at the Mariut frontal plain. Rev. Ecol. Biol. Sol 17: 327–352.

Gil, M.J, Pérez-Mellado, V., Guerrero, F. 1993. Trophic ecology of *Acanthodactylus erythrurus* in central Iberian peninsula. Is there a dietary shift? In: Valakos, E.D., Boehme, W., Pérez-Mellado, V., Maragou, P., eds. Lacertids of the Mediterranean region. Hellenic Zool. Soc., pp. 199–211.

Golley, F.B. 1961. Energy values of ecological materials. Ecology 42: 581–584.

Grimmond, N.M., Preest, M.R., Pough, F.H. 1994. Energetic cost of feeding on different kinds of prey for the lizard *Chalcides ocellatus*. Funct. Ecol. 8: 17–21.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Conn., 302 pp.

Lunn, J. 1991. Scavenging by the Madeiran lizard *Lacerta dugesii*. Br. Herpetol. Soc. Bull. 35: 10–11.

Maragou, P., Valakos, E.D., Giannopoulos, Z., Stauropoulou, A., Chondropoulos, B.P. 1996. Feeding ecology of *Podarcis peloponnesiaca* (Sauria: Lacertidae) in spring. Herpetozoa 9: 105–110.

Ouboter, P.E. 1981. The ecology of the island-lizard *Podarcis sicula salfii*: correlation of microdistribution with vegetation coverage, thermal environment and food size. Amphibia-Reptilia 2: 243–257.

Pérez-Mellado, V. 1982. Estructura de una taxocenosis de Lacertidae (Sauria: Lacertidae) del Sistema Central. Mediterranea 6: 39–64.

Pérez-Mellado, V. 1992. Ecology of lacertid lizards in a desert area of eastern Morocco. J. Zool. 226: 369–386.

Pérez-Mellado, V., Corti, C. 1993. Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). Bonn. Zool. Beitr. 44 (3–4): 193–220.

Pérez-Mellado, V., Corti, C., Lo Cascio, P. 1997. Tail autotomy and extinction in Mediterranean lizards. A preliminary study of continental and insular populations. J. Zool. 243: 533–541.

Pérez-Mellado, V., Cortazár, G., López-Vicente M., Perera, A., Sillero, N. 2000. Interactions between the Balearic lizard *Podarcis lilfordi* and the plant *Dracunculus muscivorus*. Amphibia-Reptilia 21: 223–226.

Pianka, E.R. 1971. Lizard species density in the Kalahari desert. Ecology 52: 1024–1029.

Pianka, E.R. 1973. The structure of lizard communities. Annu. Rev. Ecol. Syst. 4: 53–74.

Pianka, E.R. 1986. Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton Univ. Press, Princeton, New Jersey, 229 pp.

Pianka, E.R. 1993. The many dimensions of a lizard's ecological niche. In: Valakos, E.D., Boehme, W., Pérez-Mellado, V., Maragou, P., eds. Lacertids of the Mediterranean region. Hellenic Zool. Soc. pp. 121–154.

Pollo, C.J., Pérez-Mellado, V. 1988. Trophic ecology of a taxocenosis of Mediterranean Lacertidae. Ecol. Med. 14: 132–147.

Pollo, C.J., Pérez-Mellado, V. 1991. An analysis of a Mediterranean assemblage of three small lacertid lizards in central Spain. Acta Oecologica-Oecologia Generalis 12: 655–671.

Pough, F.H. 1973. Lizard energetics and diet. Ecology 54: 837–844.

Pulliam, H.R. 1975. Diet optimization with nutritional constraints. Am. Nat. 109: 765–768.

Quayle, A. 1983. Notes on the diet of Erhard's wall lizard, *Podarcis erhardii*. Br. J. Herpetol. 6: 309–310.

Rapport, D.J. 1980. Optimal foraging for complementary resources. Am. Nat. 116: 324–346.

Robson, G.M., Lambert, M.R.K. 1980. Observations on the insect food of some semi-desert lizards in southern Morocco. J. Arid Environ. 3: 141–151.

Roots, C. 1978. The chemical composition of the mealworm. IWRC Wild J. 1 (4): 11–12.

Sadek, R.A. 1981. The diet of the Madeiran lizard *Lacerta dugesii*. Zool. J. Linn. Soc. 73: 313–341.

Sorci, G. 1990. Nicchia trofica di quattro specie di Lacertidae in Sicilia. Naturalista siciliana, S.IV, XIV (suppl.): 83–93.

Valakos, E.D. 1986. The feeding ecology of *Podarcis erhardii* in a main insular ecosystem. Herpetol. J. 1: 118–121.

Van Damme, R. 1999. Evolution of herbivory in lacertid lizards: effects of insularity and body size. J. Herpet. 33 (4): 663–674.

Wallwork, J.A. 1976. The distribution and diversity of soil fauna. Academic Press, London. 355 pp.