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PEREZ-MELLADO, V<sup>1</sup> BAUWENS, D., GIL, M., GUERRERO, F., LIZANA, M., and CIUDAD, M.-J.

We studied diet composition and prey selection in the lizard *lacerta monticola* throughout its activity season. The most important prey groups in terms of numbers were Coleoptera, Diptera, Formicid ae. and Araneae. Comparison of diet composition in the adult lizards with estimates of prey availability indicated that lizards exhibited precisely defined patterns of prey selection. Electivity scores were negative for prey < 3 mm in length and generally positive for larger prey, despite the higher relative abundance of the former group in the environment. Electivity scores for individual prey taxa were positively correlated with their length, and lizards preferentially consumed larger individuals belonging to the taxa containing smaller animals. Relative availability of the four major prey taxa fluctuated considerably throughout the year. In spite of these changes, monthly rates of consumption of Araneae and Diptera remained almost constant. Variations in monthly electivity scores were negatively correlated with relative availability of three (Coleoptera, Diptera, and Araneae) of the four major prey taxa. These results fit the predictions of prey-selection models based on nutrient constraints.

:"Jous avons étudié la composition du régime alimentaire et la sélection des proies chez le lézard *lacerta monticola* durant toute sa saison d'activité. Les principaux groupes de proies, selon leur abondance, étaient les coléoptères, les diptères, les araignées et les araignées. La comparaison entre le régime alimentaire des lézards adultes et la disponibilité des proies indique que les lézards opéraient une prédation selon une tendance bien définie dans leur choix de proies. La sélection était négative à l'égard des proies <3 mm de longueur et généralement positive à l'égard des proies plus grandes, en dépit de l'abondance plus grande des petites proies dans le milieu. Les taxons étaient choisis en fonction de leur longueur et les lézards consommaient de préférence les individus les plus grands parmi les taxons les plus petits. La disponibilité relative des quatre principaux taxons de proies a fluctué considérablement au cours de l'année. En dépit de ces changements, les taux mensuels de consommation d'araignées et de diptères sont restés à peu près constants. Les variations dans le nombre de fois que des proies ont été choisies étaient en corrélation négative avec la disponibilité relative de trois (coléoptères, diptères et araignées) des quatre principaux taxons de proies. Ces résultats sont conformes aux prédictions des modèles de choix de proies fondés sur des contraintes nutritionnelles.

## Introduction

The vast majority of extant lizards are diurnal and insectivorous but lack obvious dietary specializations (Greene 1982). This generalization certainly applies to European lizards of the family Lacertidae, which feed on a wide variety of mainly arthropod prey (Arnold 1987 and references therein). Apart from their high dietary diversity, lacertids are believed to be opportunistic predators which do not exhibit well-defined patterns of prey selection, apart from those imposed by body size constraints (e.g., Avery 1966; Darevskii 1967; Arnold 1987; Mou 1987). Accordingly, variation in diet composition among species and populations is thought to primarily reflect differences in prey availability (Arnold 1987).

The energy requirements of lizards are an order of magnitude lower than those of similar-sized endotherms (Pough 1980; Bennett 1982). As a consequence, maximization of the net rate of energy gain, a basic assumption of many prey-selection models, might be less important for small insectivorous lizards (Stamps et al. 1981; Pough and Andrews 1985). However, few studies have actually examined the quantitative predictions of optimal foraging models, using lizards as the model predator (see review by Stephens and Krebs 1986).

We report on a study of diet composition and prey selection in a natural population of the lizard *Lacerta monticola*. We

examined (i) diet composition in different lizard age and sex classes, (ii) the extent of prey selection by comparing types and sizes of the prey eaten with those of available prey, and (iii) the relationship between seasonal changes in diet composition and prey availability. Predictions made according to different types of optimal foraging models about the relationship between prey selectivity and relative abundance of prey types in the environment have been summarized by Stamps et al. (1981). We discuss our findings in the light of these predictions.

## Material and methods

### Study animals

*lacerta monticola* is a lizard indigenous to the Iberian Peninsula, whose distribution is restricted to mountainous areas (Pyrenees, Iberian Central System) and coastal regions in the northwestern part of the Iberian Peninsula (Curt and Galán 1982; Elvira and Yigal 1982; Salvador 1984). Four subspecies, which are geographically isolated, have been described (Müller and Hellmich 1937; Salvador 1984). The lizards studied here were assigned to the form *lacerta monticola cyreni*, whose distribution is limited to high-elevation areas in the Iberian Central System.

*lacerta monticola* is a small (adult body length 55–80 mm; mass 4–12 g) heliothermic lizard which maintains body temperatures in the range 30–38°C during activity (Pérez-Mellado 1982). It is partly saxicolous and partly ground dwelling. This oviparous species has a well-defined annual activity and reproductive cycle. Mating and oviposition occur during May and July, respectively, and the young are born during August–September (Pérez-Mellado 1982). The lizards hibernate from October to the beginning of April.

<sup>1</sup>Present address: Institute of Nature Conservation, Kiewitdreef 3, B-3500 Hasselt, Belgium.

### Study area and procedures

The study area is situated in the central part of the Sierra de Gredos (province of Avila, Spain) at altitudes between 1800 and 2300 m. In this area *L. monticola* is found at heights between 1500 and 2400 m, with maximum abundance between 2000 and 2200 m (Ciudad et al. 1987). The study site, where *L. monticola* is the only lizard species present, is an alpine meadow scattered with stones and rocks.

We captured a total of 178 lizards between April and September 1986. Upon capture, lizards were injected with a buffered solution (pH 7) of formalin; after 24–48 h they were transferred to 70% ethanol. For each lizard we measured (to the nearest 0.1 mm) snout-vent length (SVL), length and width of the pileus, and head height. In the laboratory we removed the entire digestive tract and examined the different parts for the presence of prey remnants. Prey items ( $n = 1359$ ) were identified to the level of family or order. We used the length of (nearly) intact prey items ( $n = 598$ ) to estimate their size.

Three age-classes of lizards were distinguished (body-length data are summarized in Table 2): juveniles (born during the current activity season); subadults (born during the preceding year, nonreproductive); and adults (lizards in at least their third season, reproductive). We did not distinguish between the sexes in the juvenile age-class.

Estimates of the availability of potential prey for *L. monticola* were obtained through the use of pitfall and adhesive traps. The former were 1-L vessels buried up to their rims in the soil; they contained 200 cm<sup>3</sup> of a 10% formalin solution. The adhesive traps consisted of plastic Petri dishes containing a 5 mm thick layer of adhesive paste (Tanglefoot Co<sup>®</sup> Michigan) which were buried up to their top edge in the topsoil. All traps were covered with a zinc cover raised some 2.5 cm above the top. We installed five traps of each type along two parallel lines 3 m apart; the distance between successive traps was 10 m. The traps were located at an elevation of 2000 m within the habitat occupied by *L. monticola*, and the contents were collected at monthly intervals. A total of 1471 potential prey items were captured. Each was identified and its length was measured. We assume that the relative abundances of the different prey types in the traps reflect their availability to the lizards. There is no way to test the validity of this assumption, as prey availability depends not only on abundance but also on behaviour. Hence, arthropod groups differ in their catchability according to the trapping technique used (Southwood 1976). For instance, pitfall traps yield the highest numbers of ground-dwelling prey (e.g. Araneae, Coleoptera, Formicidae, insect larvae), whereas flying taxa (e.g. Diptera, Homoptera, Lepidoptera) are more often caught in the adhesive traps (Heulin 1985; personal observations). We reduced this type of sampling bias by pooling the prey trapped by the two techniques. In addition, an important part of our analysis focuses on seasonal changes in the relative abundances of certain prey taxa. For these analyses we must assume that a constant proportion of these prey was trapped throughout the activity season, irrespective of their actual availability to the lizards (Stamps et al. 1981).

Diet composition and prey availability were analysed with respect to both taxonomic status and size of the prey items. We quantified the contribution of a prey type to the diet by calculating two indices: relative abundance (percentage of total prey numbers corresponding to a given prey type) and relative incidence (percentage of stomachs containing a given prey type). Trophic (prey taxon) diversity was calculated using Levins' index of niche breadth (Levins 1968). Prey size diversity was calculated with the same index, after grouping prey into 16 length classes (the first 8 classes represented 1-mm intervals and the remaining 8 classes represented 3-mm intervals). Overlap in diet composition (prey taxa) was estimated using the symmetric index of Pianka (1978). Prey electivity was calculated with Ivlev's (1961)  $I$  index as modified by Jacobs (1974). This index was specifically designed for comparing selectivity with the availability of prey types in the environment. Because we consider and analyse preference ranking rather than absolute electivity values, our results should be comparable to those given by other electivity indices (Lechowicz 1982). Correlations between electivity values and prey availability were estimated by means of a nonparametric technique (Spearman rank correlation,  $r_s$ ),

to reduce the possible effects of sampling bias in estimating prey availability. All prey length data were logarithmically transformed before statistical treatment. We calculated average prey length and its confidence limits using logarithmically transformed data: the back-transformed confidence intervals are therefore asymmetrical around the mean (Sokal and Rohlf 1969).

## Results

### Composition of the diet in terms of taxa

With respect to both relative abundance and relative incidence, Coleoptera were the most important prey group, followed by Diptera, Formicidae, and Araneae (Table 1). The data reveal a significant positive rank correlation between relative abundance and relative incidence of prey items (Table 1;  $P < 0.01$  in all age and sex groups of lizards), indicating that the most frequently eaten prey were encountered in a large proportion of the stomachs examined. Hence, the high relative abundance of a prey group is not due to the sporadic finding of many items in a few stomachs.

The relative contribution of Coleoptera to the diet seemed to increase, whereas that of Diptera and Araneae decreased, with lizard age (Table 1). Trophic diversity was highest in the younger age-classes (Table 1), although these preyed upon a smaller number of prey taxa than the adults did. The higher diversity values for juveniles and subadults should therefore be attributed to greater consistency in the prey taxa eaten. The estimates of dietary overlap ( $O$ ) indicate greater similarity in diet composition between adult males and females ( $O = 0.94$ ) than between adults and juveniles (adult males–juveniles:  $O = 0.68$ ; adult females–juveniles:  $O = 0.81$ ). The most notable difference between adult males and females is the higher contribution of Diptera to the females' diet.

### Prey size

There were marked differences in the size of prey eaten by lizards of different age and sex classes (Table 2; ANOVA of  $\ln$  prey size:  $F = 27.62$ ,  $P < 0.001$ ). Mean prey length was greatest for the adult lizards. The size range of prey consumed also tended to increase with age of the lizard.

A comparison of the different age and sex classes of lizards reveals positive rank correlations between mean prey length and the average values for various morphometric traits (Table 2; SVL:  $r_s = 0.90$ ; length and width of pileus, head height:  $r_s = 0.80$ ; all  $P < 0.05$ , one-tailed test).

### Food availability and electivity

Considering the differences in diet composition among age-classes, we restricted all further analyses to the adult lizards, for which sample sizes were largest.

Acarida, Diptera, Araneae, and Formicidae were the most abundant arthropods in the traps (Table 3). Electivity scores for the different prey taxa were highly coincident among adult males and females ( $r_s = 0.840$ ,  $P < 0.001$ ). Electivities were highest for Plecoptera and Trichoptera, although these groups were poorly represented in both the lizards' diet (Table 1) and the traps (Table 3). Acarida and Diptera had the lowest electivities. Coleoptera, which were important prey for all lizard groups, exhibited high electivity scores. For other important prey taxa such as Formicidae, Diptera, and Araneae, electivity scores were close to zero or negative.

We examined correlations between the electivities of the different prey taxa and their relative abundance in the environment. Significant negative correlations were evident for both

TABLE 1. Relative abundance (%rel.) and relative incidence (%inc.) of various prey taxa, number of prey items, number of lizardsexamined, prey taxon diversity, and rank correlation between relative abundance and relative incidence (r) for *L. monticola* in different age and sex classes

Prey taxon	Subadults						Adults				Total	
	Juveniles		Males		Females		Males		Females			
	rel.	inc.	%rel.	%inc.	%rel.	%inc.	%rel.	inc.	%rel.	inc.	rel.	inc.
Opiliona			3.3	6.7			1.1	8.3	0.7	3.3	0.9	5.2
Araneae	24.1	60.0	11.5	40.0	22.9	66.7	7.5	40.3	10.0	51.7	10.9	47.7
Acarida	12.7	20.0			2.8	13.3	0.2	1.4	0.2	1.7	1.1	3.5
Diplura	—						0.2	1.4	0.2	1.7	0.1	1.2
Thysanura	1.3	10.0	1.6	6.7	0.9	6.7	0.2	1.4	0.7	3.3	0.6	3.5
Myriapoda	2.5	10.0					0.7	5.6	1.3	10.0	1.0	6.4
Ephemeroptera							0.2	1.4	0.2	1.7	0.1	1.2
Dermaptera							0.9	4.2	0.5	5.0	0.6	3.5
Dyctioptera			3.3	13.3			0.2	1.4	0.2	1.7	0.3	2.3
Trichoptera	1.3	10.0	1.6	6.7	1.8	6.7	5.1	8.3	2.0	13.3	3.2	9.9
Plecoptera	1.3	10.0			0.9	6.7	2.2	16.7	4.1	13.3	2.7	12.8
Homoptera	3.8	30.0	14.8	33.3	7.3	33.3	3.5	20.8	3.9	26.7	4.5	25.6
Coccidae							0.5	2.8	4.1	1.7	1.9	1.7
Heteroptera	3.8	30.0	3.3	13.3			3.1	20.8	2.5	21.7	2.6	19.2
Orthoptera			4.9	20.0	0.9	6.7	1.3	6.9	2.0	16.7	1.6	11.0
Formicidae	8.9	40.0	4.9	20.0	6.4	13.3	12.8	33.3	11.1	36.7	11.0	32.0
Hymenoptera	2.5	20.0	3.3	13.3	2.8	20.0	6.6	25.0	3.6	25.0	4.6	23.3
Lepidoptera			6.6	26.7	1.8	13.3	1.3	6.9	1.6	11.7	1.6	10.5
Larval Lepidoptera	1.3	10.0			0.9	6.7	1.3	9.7	0.5	5.0	0.9	7.0
Coleoptera	16.5	60.0	19.7	46.7	25.7	86.7	35.7	81.9	27.9	85.0	29.8	79.1
Larval Coleoptera			3.3	6.7	0.9	6.7	4.2	22.2	2.3	16.7	2.9	16.3
Diptera	20.3	60.0	9.8	20.0	21.1	66.7	7.7	34.7	16.3	46.7	13.1	41.9
Larval Diptera			1.6	6.7			1.8	2.8	2.3	5.0	1.8	3.5
Insecta (undetermined)							1.3	8.3	0.4	3.3	0.8	4.7
Larval Insecta			3.3	6.7	0.9	6.7	0.4	2.8	1.1	6.7	0.8	4.7
Arthropoda (undetermined)			3.3	13.3	1.8	6.7	0.2	1.4	0.4	3.3	0.4	3.5
Gastropoda							0.2	1.4	0.2	1.7	0.2	1.2
No. of prey items	79		61		109		549		560		1359	
No. of lizards examined	10		15		15		72		60		172	
Diversity	0.456		0.558		0.313		0.191		0.245		0.238	
r	0.926		0.921		0.933		0.953		0.842		0.883	

TABLE 2. Length of prey, prey size diversity, and morphometric characteristics of *L. monticola* in different age and sex classes

	Body length of prey (mm)	Diversity	n	SVLb	Lpb	HHb	WPb	N
Juveniles	2.48; 2.05-3.00 (1.3-14.1)	0.395	37	34.60±4.24	8.52±0.93	3.55±0.43	4.16±0.38	20
Subadults								
Males	2.65; 1.90-3.70 (1.0-9.9)	0.561	21	52.50±3.85	12.79±0.75	5.14±0.33	5.76±0.32	9
Females	3.34; 2.98-3.75 (1.5-9.0)	0.369	52	54.63±4.33	12.11±0.79	5.09±0.43	5.53±0.33	12
Adults								
Males	5.23; 4.86-5.63 (1.5-22.6)	0.643	257	70.56±5.06	17.05±1.45	7.48±0.55	7.65±0.55	84
Females	5.47; 5.10-5.87 (1.0-30.0)	0.305	231	69.95±5.40	14.52±1.32	6.25±0.43	6.60±0.42	70

NOTE: n, number of prey measured; SVL, snout-vent length; LP, length of the pileus; HH, head height; WP, width of the pileus; N, number of lizards measured.  
 \*values are given as the mean, followed by 95% confidence limits, with the range in parentheses.  
 •values are given as the mean ± SD.

TABLE 3. Relative abundance of different prey taxa in the trap, electivities by adult males and females, and mean length in traps and in stomachs of adults

Prey taxon	Relative abundance (%)	Electivity		N	Mean length (mm)		
		Males	Females		Traps	N	Stomachs
Opilionida	2.2	-0.70	-1.13	32	2.07		
Araneae	16.5	-0.89	-0.57	212	4.33	39	4.03
Acarida	24.7	-5.19	-5.21	364	1.00		
Thysanura	0.4	-0.81	0.56				
Myriapoda	0.7	0.07	0.61	10	10.34		
Derrnaptera	1.1	-0.18	-0.71	16	8.78		
Dyctioptera	3.0	-2.83	-2.85	44	4.31		
Trichoptera	0.1	3.68	2.69				
Plecoptera	0.1	3.49	4.14				
Homoptera	4.1	-0.19	-0.06	61	2.40	12	3.20
Heteroptera	0.7	1.44	1.22	11	3.08		
Onhoptera	1.3	-0.01	0.43	19	10.34		
Formicidae	10.2	0.25	0.09	150	4.12	51	6.12
Hymenoptera	2.4	1.06	0.42	35	2.42	13	10.15
Lepidoptera	1.3	-0.01	0.22	19	5.43		
Coleoptera	5.8	2.19	1.83	86	6.14	211	5.53
Larval Coleoptera	1.2	1.32	0.71	17	8.29	32	7.90
Diptera	19.4	-1.06	-0.21	285	3.24	33	4.75
Insecta (undetennined)	2.6	-0.72	-2.00	88	2.66		
Larval Insecta	1.4	-1.33	-0.24	20	1.07	18	9.57
Anthropoda (undetermined)	0.9	-1.59	-0.91	13	2.11		

NOTE: Prey length is shown only for taxa for which 2-10 measurements were obtained.

TABLE 4. Relative abundance (%rel.) of different prey size classes in traps and in stomachs of adult lizards, and their electivities (elect.) by adult lizards

Prey size (mm)	%rel. in traps	Adult males		Adult females	
		%rel.	Elect.	%rel.	Elect.
0-1	14.5	0.0		0.0	
1-2	18.2	2.3	-2.23	2.2	-2.30
2-3	19.2	16.7	-0.17	3.9	-1.77
3-4	10.1	11.3	0.12	10.4	0.03
4-5	10.3	12.8	0.25	17.3	0.60
5-6	4.4	10.1	0.91	36.4	2.53
6-7	9.2	7.0	-0.30	7.4	-0.25
7-8	5.0	10.9	0.85	3.9	-0.25
8-11	4.0	18.7	1.70	6.9	0.58
11-14	3.0	5.1	0.55	3.5	0.15
14-17	1.5	3.9	0.98	1.7	0.15
17-20	0.2	0.4	0.65	2.2	2.38
20-23	0.3	0.8	1.06	2.6	2.28
23-26	0.1	0.0		0.4	1.85
26-29	0.1	0.0		0.4	1.85
>29	0.0	0.0		0.9	
No. of prey measured	1471	257		231	

sexes (adult males:  $r = -0.459, P < 0.05$ ; adult females:  $r = -0.564, P < 0.02$ ), indicating that lizards did not select prey taxa in proportion to their relative abundance in the environment.

The size distribution of the available prey was skewed towards the smaller length classes (Table 4). Electivity increased with prey size class (males:  $r = 0.727, P < 0.02$ ; females:  $r = 0.573, P = 0.05$ ) but decreased with relative abundance in the traps

(males:  $r = -0.743, P < 0.02$ ; females:  $r = -0.664, P < 0.05$ ). Thus, lizards selected prey of the larger size classes despite their relative scarcity in the environment (the relative abundances of prey in the traps decreased exponentially with the size class;  $r = -0.967, P < 0.001$ ). Further examination of the data (Table 4) indicates that electivities did not increase continuously with prey size. Electivity scores were negative for prey <3 mm long, and generally positive for prey 2-3 mm long. For prey 2-3 mm long no significant increase in electivity with prey size could be detected (males:  $r = 0.576, P > 0.05$ ; females:  $r = 0.396, P > 0.10$ ).

To what extent did lizard preference for certain prey taxa depend upon the size of the prey? We found positive rank correlations between the electivity scores of different prey taxa and the mean length of individuals in the traps (males:  $r = 0.517, P < 0.05$ ; females:  $r = 0.534, P < 0.05$ ; analysis was restricted to 18 prey taxa for which 2-10 items were measured; Table 3). For all taxa with a mean length <3 mm electivity scores were negative, whereas for the larger prey groups electivity scores were variable and not a simple function of the size of the prey. Furthermore, the difference between the average lengths of prey of the various taxa in the stomachs and in the traps was negatively correlated with the mean length of those in the traps ( $r = -0.762, P < 0.05$ ; analysis was restricted to eight prey taxa for which 2-10 items were measured in both traps and stomachs; data for adult males and females were pooled; Table 3). Hence, lizards tended to reject the small individuals within a taxon, and to prefer the larger individuals from that taxon.

The importance of prey length was further examined within each of the four most important prey taxa (Coleoptera, Diptera, Formicidae, and Araneae). For three (Coleoptera, Diptera, Formicidae), variance in length of the available prey significantly exceeded that of the prey eaten (F-test,  $P < 0.01$ ). For

TABLE 5. Monthly variation for the four major prey taxa in relative abundance in stomachs of adult lizards, electivity by adult lizards, relative abundance in the traps, and mean length in the traps

	April	May	June	July	August
<b>Araneae</b>					
Relative abundance (%)					
Traps	11.7	11.1	22.3	17.5	22.7
Stomachs	11.9	12.0	5.2	8.9	5.7
Electivity	0.01	0.04	-0.72	-0.97	-0.69
Mean length (mm)	3.39	4.01	4.76	5.16	3.71
<b>Formicidae</b>					
Relative abundance (%)					
Traps	3.9	11.7	11.8	15.0	25.3
Stomachs	4.8	1.2	0.9	17.8	30.5
Electivity	0.09	-1.04	-1.15	0.09	0.11
Mean length (mm)	3.03	3.29	4.01	5.47	4.35
<b>Coleoptera</b>					
Relative abundance (%)					
Traps	1.9	1.8	5.8	10.8	13.1
Stomachs	50.0	43.8	46.9	22.3	11.4
Electivity	1.70	1.64	1.16	0.37	-0.07
Mean length (mm)	3.49	4.76	5.37	9.39	5.53
<b>Diptera</b>					
Relative abundance (%)					
Traps	56.3	56.1	23.6	2.5	8.3
Stomachs	7.1	5.6	8.9	11.3	11.4
Electivity	-1.22	-1.33	-0.50	0.70	0.15
Mean length (mm)	3.32	4.57	1.97	3.42	3.67

the Formicidae and Diptera, mean prey length in the stomachs was significantly greater than mean length of the available prey (t-test,  $P < 0.005$ ). These analyses indicate that lizards consumed the larger individuals of the Formicidae and Diptera available, and seemed to prey upon all but the smallest and largest Coleoptera. We found no evidence of selection for length within the Araneae. It is noteworthy that Araneae 1-3 mm long constituted 33% of all spiders consumed, which is directly proportional to their relative abundance in the traps (31%).

#### Seasonal variation in diet composition and prey availability

We restricted our analyses to the period April-August and to the four most important prey taxa (Araneae, Formicidae, Coleoptera, Diptera), whose pooled monthly contribution to the diet fluctuated between 60 and 74%. Adult males and females showed very similar trends in monthly diet composition and prey electivities, so data for both groups were pooled. Acarida were excluded from the monthly prey availability estimates, as they were seldom eaten by the lizards (Table 1) and their relative abundance in the traps exhibited large seasonal fluctuations.

The relative abundance of Formicidae and Coleoptera in the diet exhibited considerable seasonal variation (G-test, both  $P < 0.001$ ), whereas the relative abundance of Araneae ( $G = 8.893$ ,  $P = 0.06$ ) and Diptera ( $G = 7.669$ ,  $P > 0.10$ ) remained fairly constant throughout the activity period (Table 5). The relative contribution of Formicidae was highest during the midsummer months (July, August), whereas Coleoptera formed the bulk of the diet during April-June (Table 5).

The relative abundance in the traps of all four prey groups fluctuated dramatically throughout the year (G-tests, all  $P < 0.001$ ; Table 5). We examined whether variations in electivity of prey taxa tracked seasonal fluctuations in their availability. Only

for the Formicidae did we find a positive, nonsignificant rank correlation ( $r = 0.46$ ,  $P > 0.30$ ). For the other taxa, monthly electivities were negatively correlated with their relative abundance in the traps ( $r = -0.90$ ,  $P = 0.07$  for the three groups). A negative relationship between electivity and relative abundance in the habitat can arise under several conditions (Stamps et al. 1981). The relative contribution of Araneae and Diptera to the diet did not vary significantly among months (from 5 to 12%; Table 5). Hence, lizards ate an approximately constant proportion of these prey types which was independent of large fluctuations in their relative availability. This produces the negative relationship observed for Araneae and Diptera between electivity and relative abundance in the traps. For Coleoptera, a nonsignificant negative rank correlation was found between monthly relative abundance in the stomachs and in the traps ( $r = -0.700$ ,  $P > 0.10$ ). In addition, the slope ( $b = -0.152$ ,  $SE = 0.006$ ) of the relationship between monthly electivity scores and relative abundance in the habitat was significantly more negative ( $t = 10.935$ , 3 df,  $P < 0.01$ ) than the slope ( $b = -0.083$ ) expected on the basis of a constant relative abundance in the lizards' diet (see Stamps et al. 1981 for details of methodology). These results indicate that the selectivity of Coleoptera decreased as their relative abundance in the environment increased.

The size of the prey eaten by adult lizards varied significantly among months, but we found no difference between the sexes (two-way ANOVA of ln prey size; month:  $F = 8.587$ ,  $P < 0.001$ ; sex:  $F = 0.398$ ,  $P > 0.50$ ; interaction:  $F = 1.525$ ,  $P > 0.10$ ). Prey length tended to increase throughout the activity season (Table 6).

We compared the lengths of the prey consumed by adult lizards (males and females pooled) during different months with

TABLE 6. Monthly variation in length of prey (mm) encountered in stomachs of adult lizards and in the traps

	<i>N</i>	Stomachs	<i>N</i>	Traps
April	22	5.06: 4.23-6.06 ( 1.0-7.6)	103	3.19: 2.86-3.56 ( 1.5-12.5)
May	147	4.37; 4.02-4.74 {1.5-18.0)	171	3.97: 3.64-4.34 ( 1.5-30.5)
June	129	5.42: 4.95-5.93 ( 1.5-28.5)	382	3.10: 2.85-3.36 (0.5-21.5)
July	149	6.01: 5.45-6.63 ( 1.3-30.0)	120	5.21: 4.60-5.89 (0.5-21.5)
August	36	7.03; 5.44-9.09 (2.0-21.8)	229	4.48: 4.15-4.84 (0.5-15.5)

NOTE: Values are given as the mean, followed by 95% confidence limits, with the range in parentheses. Ararida were excluded from the trap samples. *N* is the number of items measured.

those of arthropods captured in the traps (excluding Acarida). A two-way ANOVA revealed a difference between prey encountered in the stomachs and in the traps ( $F = 68.196$ ,  $P < 0.001$ ), a significant variation among months ( $F = 21.076$ ,  $P < 0.001$ ), and a significant interaction effect between these two factors ( $F = 7.275$ ,  $P < 0.001$ ). The last result indicates that the difference in length of the prey encountered in stomachs and traps varies among months: during June, April, and August, the mean length of the prey eaten by the lizards was much greater than that of the prey trapped (Table 6).

To further examine seasonal variation in prey size, prey were assigned to one of three length classes:  $< 3$ ,  $3-8$ , and  $\geq 8$  mm. The relative abundance of these prey size classes varied among months in both the stomachs and the traps (G-tests, all  $P < 0.001$ ). Monthly electivity scores were negatively correlated with the relative abundance in the traps of prey  $< 3$  mm ( $r_s = -0.90$ ,  $P = 0.07$ ) and  $3-8$  mm ( $r_s = -1.00$ ,  $P < 0.05$ ) in length, whereas no correlation was found for the greatest-length category ( $r_s = 0.30$ ,  $P > 0.50$ ). These results indicate that lizards did not increase their selectivity towards the largest prey as the relative abundance of the Jatter in the habitat increases.

Finally, we investigated the extent to which seasonal variation in electivity scores for the four major prey taxa was related to fluctuations in their size. In none of the four taxa did we find significant rank correlations between electivity scores and average monthly size or relative size (mean length of taxon minus mean length of all prey consumed in a given month). In fact, six of eight correlations were negative.

#### Discussion

Our results on composition of the diet of *L. monticola* agree reasonably well with those of previous studies (Martinez-Rica 1977; Dominguez et al. 1982; Pérez-Mellado 1982). All these reports established that Coleoptera, Diptera, Araneae, and Formicidae are numerically the most important prey of this lizard. Relative abundance scores for Hymenoptera (other than ants), Homoptera, and Heteroptera were rather high in some studies (Martinez-Rica 1977; Pérez-Mellado 1982).

Some differences were found among age and sex groups of lizards, with respect both to the taxonomic composition of the diet and to prey size. Juveniles and subadults preyed upon a relatively low number of taxonomic groups, but these were more equally represented than in the adults' diet. Both average length

and size range of the prey eaten increased with age of the lizard. Hence, although Jarger lizards ate the biggest prey items, they did not exclude the smaller prey from their diet. Similar observations have been reported for other lacertid lizards (e.g., Nourira and Mou 1982; Jou and Barbault 1986; Mou 1987). The diets of adult males and females were very similar, except that females consumed a Jarger proportion of Diptera. The findings of Pérez-Mellado (1982) were similar for other populations of *L. 1110nticola*.

Our most interesting results emerge from the comparison of the relative abundances of different prey types in the lizards' stomachs and in the traps. Assuming that the relative abundances of prey groups in the traps reflect their availability in the habitat, our results indicate that diet composition is in no way a simple reflection of food availability. This result challenges the opinions of other students of the feeding habits of lacertid lizards (Avery 1966; Darevskii 1967; Arnold 1987), who often did not consider prey availability. *Lacerta 1110nticola* seemed to exhibit a strong preference for Coleoptera, whereas Acarida, the most abundant arthropods in the habitat, were seldom captured. It has previously been suggested that Coleoptera are the preferred prey of *L. monticola* (Pérez-Mellado 1981), although this interpretation has remained speculative in the absence of estimates of prey availability. Our data confirm this suggestion. Analysis of the total lizard sample showed that other important prey groups, such as Formicidae, Araneae, and Diptera, seem to be eaten in proportion to their relative abundance. However, monthly variation in the relative abundance in the diet of the latter two prey groups, did not track changes in their relative abundance.

What do our data tell us about food selection by this lizard? They indicate that prey size is an important factor guiding prey choice by *L. monticola*. Lizards select arthropods of the larger size classes, electivity scores are highest for the larger prey taxa, and they consume larger individuals from the taxa containing smaller prey. Evidence for prey-length selection was also obtained from three of the four major prey groups (Coleoptera, Diptera, Formicidae). The Araneae are a notable exception: a large proportion of the spiders eaten are  $< 3$  mm long, whereas for other prey taxa these length classes are very underrepresented in the lizards' diet.

Many optimal foraging models assume that a foraging predator tends to maximize the rate of net energy intake (e.g., Schoener 1971; Pyke et al. 1977; Stephens and Krebs 1986). The net energy value of a prey item is the difference between its energy content and the energy expended in its capture and manipulation. Pough and Andrews (1985) have demonstrated that the energy cost for a lizard of pursuing, subduing, and swallowing a prey item is negligible relative to the prey's energy value. The size of arthropods, a crude though useful index of their energy content (Schoener 1971; Werner 1974; Stampset al. 1981), will therefore provide a reliable estimate of net energy gain. Hence, net energy intake should be highest for larger prey. However, the abundance of arthropod prey decreases as their size increases (Table 4; see also Schoener and Janzen 1968), and the time required for lizards to subdue and swallow a prey item increases faster than prey size (Pough and Andrews 1985). As a consequence, net energy gain per unit time spent foraging by lizards presumably declines monotonically with increasing prey size (Pough and Andrews 1985). In other words, if lizards tend to maximize their rate of net energy intake, we would expect them to select the smaller, more abundant prey. Our results do not fit these predictions. Adult *L. monticola* avoided prey  $< 3$  mm in length, which had the highest relative abundance in the traps,

and exhibited positive though variable electivities for prey 2-3 mm long. This suggests that there existed a threshold value for prey length, about 3 mm: smaller prey tended to be rejected, whereas larger arthropods were likely to be consumed, although selectivity did not further increase with the size of prey. We tentatively conclude that maximization of net energy intake per unit feeding time is not of paramount importance for prey selection by *L. monticola*.

How do lizards respond to seasonal changes in the abundance of different prey types? Stamps et al. (1981) discuss predictions regarding the relationship between selectivity and relative abundance in the habitat for different prey types made on the basis of three groups of theoretical models of food selection: (i) prey switching, (ii) energy optimization, and (iii) nutrient optimization.

Prey-switching models (Murdoch 1969, 1973) predict that a predator will preferentially consume the most abundant prey, and switch among prey types as their relative abundance in the habitat changes. Hence, the prey-switching model predicts that for any prey type, electivity will be positively correlated with its relative availability. Our data do not fit this prediction: seasonal variation in electivity was negatively correlated with monthly relative abundance in the habitat of three of the four major prey groups. Only for Formicidae did we find a positive but nonsignificant correlation between their monthly electivity and relative abundance in the traps.

Several models of energy optimization predicts that selectivity of the most valuable food types will increase with their relative abundance (Rapport 1971; Estabrook and Dunham 1976; Hughes 1979). Assuming that prey size provides a reliable estimate of energy value, we would expect a positive correlation between electivity scores for the larger prey and their relative abundance in the traps. We found no evidence for such a relationship: for prey 3-8 mm long the correlation was negative, whereas a low (nonsignificant) positive correlation was found for the largest prey size class (>8 mm). In addition, electivity scores for the four major prey groups were not related to their size.

A third group of theories considers foraging optimization on the basis of the assumption that animals attempt to obtain a balanced diet, which is achieved by consuming minimal proportions of certain prey types or nutrients (Belovsky 1981; Westoby 1978; Pulliam 1975; Rapport 1980). These models predict that the consumption rates of food types that are essential for a balanced diet will be constant, irrespective of their availability. This translates into an expected negative correlation between electivity for a given prey type and its relative abundance in the habitats (Stamps et al. 1981). Our results met this prediction by revealing a negative correlation between electivity and relative abundance in three of the four major prey groups (Araneae, Diptera, Coleoptera). Lizards consumed approximately constant proportions of Araneae and Diptera throughout the activity season, in spite of large fluctuations in their relative abundance in the habitat. It is worth recalling that lizards did not show a preference for certain size classes of Araneae, and included a considerable proportion of small (<3 mm) spiders in their diet. Selectivity of Coleoptera declined as their relative abundance in the habitat increased.

These results strongly suggest that *L. monticola* attempted to maintain a balanced diet by including minimal proportions of Araneae, Diptera, and Coleoptera in response to seasonal changes in the availability of these presumably nutritionally important food types. A similar conclusion was reached by Stamps et al. (1981) in their study of prey selection by juveniles

of the lizard *Anolis aeneus*. It is usually assumed that different types of insect prey are nutritionally equivalent, varying only in their energy value. The validity of this assumption can be questioned in the light of experimental demonstrations of enhanced survival, fecundity, or growth of insectivorous spiders (Greenstone 1979; Miyashita 1968), lizards (Vogel et al. 1986), and birds (Krebs and Avery 1984) when fed on mixed diets of natural prey rather than on pure diets. However, we are not aware of any studies that have directly assessed the nutrient contents of different arthropod groups.

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