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Basin Lacertid Lizards
A BIOLOGICAL APPROACH

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What are they really eating?

Stomach *versus* intestine as sources of diet information in lacertids

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Abstract. In many studies on lizard diet, the content of the complete digestive tract is analysed as a whole assuming that the differences between stomach and intestine are irrelevant. The hypothesis that stomach represents the real diet more accurately and uniformly than intestine is tested using a coastal population of the lacertid *Psammodromus hispanicus* as a model. Some types of preys, especially Coleoptera, were misrepresented in the intestine. Diversity tended to be either larger or lower in the intestine than in the stomach for most individuals. Estimations of population diversity were less precise and values were lower, especially for small samples (<40). Moreover, the smallest and the largest preys were underestimated which reduced the range of prey size variation. The impoverishment in small, soft preys and the undermeasurement of large preys in the intestine are due to the digestive process that decreases the possibilities of identification differentially. So, the intestine content can be considered as biased when compared with the stomach one. Results from intestine should be interpreted with caution and it is recommended that these sources of information should not be mixed. Finally, some other recommendations and predictions are added to describe the diet of the lizards.

Key words. Diet analysis, stomach, intestine, Lacertidae, lizards.

Introduction

Amongst the different sources of information on lizard diet, the direct analysis of the content of the digestive tract has been claimed to be the most reliable (Pérez-Mellado, 1987). Despite their conservation advantages, other non-invasive techniques like direct observation, stomach flushing and analysis of faeces show limitations and often produce biased results when estimating the real diet (Legler and Sullivan, 1979, Campbell and Christian, 1982, Andreu, 1988, Joly, 1988). Specifically, faeces have been considered of limited utility (Seva,

1982) because the digestive process involves many qualitative and quantitative changes between ingestion and defecation, which may decrease or to bias the possibilities of prey identification. Nevertheless, the same effect is also likely to occur when analysing different portions of the same digestive tract.

In many studies on lizard feeding habits, the content of the complete alimentary canal is analysed as a whole assuming that the differences between stomach and intestine portions are irrelevant (see for instance, Itä-mies and Koskela, 1971). However, it has conversely

been pointed out that the stomach may represent the real diet more accurately and more uniformly than intestine (Seva, 1982, Carretero and Llorente, 1991a, 1993b). The digestive process could reduce the identification opportunities when preys progress throughout the digestive tract and this probably may not be uniform, but depend on the type and size of the prey as a function of its digestibility.

These ideas were tested using a coastal population of the lacertid *Psammodromus hispanicus* as a model. The (stomach) diet of this species is well known (see Carretero and Llorente, 1991 a). It was selected because of the large number of lizards available and its euryphagy (the highest diversity amongst the NE Iberian lizards, Carretero, 1993). So, the low relative contribution of every kind of prey allowed the possible negative effects to arise but, simultaneously, the sample size was large enough to maintain the power of the comparison tests.

Material and methods

The study area was a narrow sand bar covered by psammophile vegetation with low diversity sited in El Prat de Llobregat, a coastal locality of the Llobregat delta, south of Barcelona (UTM 31TDF2370, see Carretero and Llorente, 1991a and b, for a complete description). *Psammodromus hispanicus* was the only lacertid found, reaching densities of 18 ind./Ha (Carretero, 1992). The littoral Mediterranean climate allows lizards to remain active throughout the year (Carretero and Llorente, 1993a). This species attains sexual maturity in the first year of age and usually does not survive its second year (Carretero and Llorente, 1991b).

215 lizards were collected in 1986 and 1987 in monthly campaigns during the period of maximum daily activity. At the laboratory, their snout-vent lengths (SVL) were measured using a digital calliper (0.01 mm precision). Animals were injected with 70% ethanol and stored in that liquid. These specimens were used not only in the study of feeding ecology but also in the analysis of the biometry and reproduction (Carretero and Llorente, 1991b; Carretero, 1994).

Stomach and intestine contents were analysed separately under a binocular dissecting microscope. The minimum numbers criterion (Vericad and Escarré, 1976)

was used in the prey counting of each digestive portion. Preys were identified using determination keys and the Order level was used as operational taxonomic unit (OTU, Sneath and Sokal, 1973) with some exceptions (see Figures and Tables). Prey lengths were measured using a micrometer eyepiece or a calliper (0.01 mm precision) and grouped into classes of 1 mm of interval (see figures and tables).

Jover's method (Jover, 1989) was used in the statistical analysis of diet description and trophic diversity. Four diet descriptors were calculated: the abundance (%P), the occurrence (%N), the probabilistic index (IP) or I'' (Ruiz and Jover, 1981) and the resource use index (IU, Jover, 1989).

The last one emphasises the homogeneity as the feature which must be measured by a trophic descriptor (see their advantages in Jover, 1989; see also Carretero and Llorente, 1991, 1993b, Carretero *et al.*, this volume, for examples of application of this index to the diet of lacertids).

In order to quantify the variation of the different types of prey from the stomach to the intestine, the Ivlev electivity index (Ivlev 1961, modified by Jacobs, 1974) was applied to the IU values of both portions. The electivity (Ei-s in text and tables) was calculated considering the stomach diet as the "trophic availability" of the intestine.

Margalef's diversity index (Brillouin's index for diet) was used according to Pielou (1966, 1975) and Hurtubia (1973). Mean individual diversity (Hi), population diversity (Hp) estimated by the Jack-knife technique (Jover, 1989) and total accumulated diversity (Hz) were calculated. Estimations of population diversities should be compared by t-tests (Magurran, 1988, Jover, 1989, Carretero and Llorente, 1991a). In order to observe the evolution of diversity values with the sample size, the accumulated functions for the maximum-minimum and minimum-maximum ordinations were plotted for the stomach and the intestine. The area between these cumulative curves can be considered as an estimator of the variability degree of diversity (Ruiz and Jover, 1981, Ruiz, 1985, Llorente *et al.*, 1986).

Results

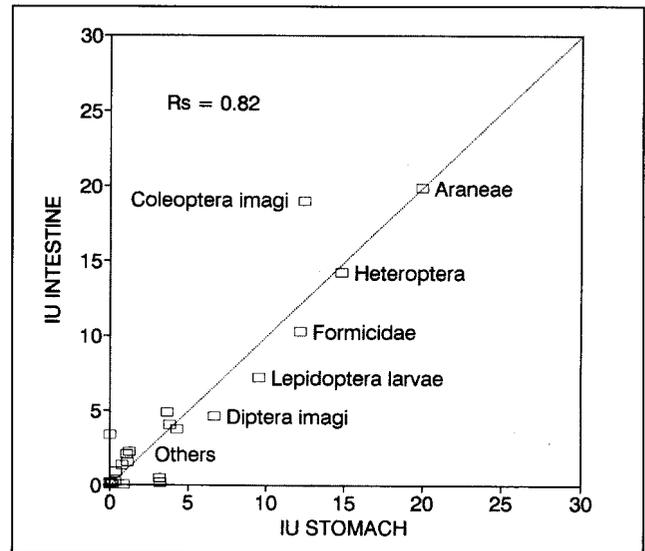
4 of the 215 lizards dissected had empty stomachs and another individual showed an empty intestine. 1076 and 881 prey items were determined in the stomachs and the intestines respectively. The numbers of preys in each compartment were correlated ($R_s=0.38$, 213 d.f., $p<0.01$). The values in the stomach were significantly higher than those in the intestine (means: 5.00 and 4.10, respectively; Wilcoxon matched pairs test, $T=5633.5$, $p=7 \times 10^{-5}$).

Table 1 shows the comparative values of the trophic descriptors for the different prey taxa. It is important to remark that four OTUs found in low numbers in the stomach (Stylommatophora, Acari, Microcoriphia and insect eggs) were completely absent from the intestine contents. It is noteworthy that the inverse case did not occur. The representation of other minority preys in the intestine tended to be strongly divergent from those of the stomach, thus producing highly positive or negative values of electivity (see Table 1). However, the major bias was detected in the main preys (see Figure 1). In fact, the importance of Coleoptera imagi increased considerably in the intestine ($E_i-s=0.21$). To a lesser extent, the inverse effect was detected for Diptera imagi ($E_i-s=-0.19$) and Lepidoptera larvae ($E_i-s=-0.14$) which decreased its representation. Consequently, the absolute values of the taxonomic composition were significantly different in the two digestive portions ($G=14.33$, 6 d.f., $p=0.026$). Looking at the standard residuals of the crosstabs, only the difference in Coleoptera was significant ($p<0.05$).

The diversity values are shown in Table 2. Although stomach and intestine did not differ significantly in their individual diversities, it was found that both values were correlated (see Figure 2, $R=0.50$, 213 d.f., $p<0.01$) and the slope of the regression line was significantly different from 1 ($T=11.21$, 213 d.f., $p=1.13 \times 10^{-17}$). The population diversities could not be directly compared since variances lacked homocedasticity. In fact, the variation of the jack-knife estimation for the intestine was higher than that for the stomach ($F=1.77$, 213, 210 d.f., $p=1.7 \times 10^{-5}$, see Table 2). However, the cumulative plot of the diversities always showed the lines of the stomach above the intestine lines (Figure 3). The increment pattern of cumulated diversity was highly divergent between both digestive compartments up to 40-45 contents (see Figure 3). Higher numbers of contents

gives more similar patterns.

The trophic descriptors for the different prey sizes are shown in Table 3. Conversely to the taxonomic analysis, no great differences in the general distribution and the modal values were observed, both histograms followed the typical logarithmic shape (Figure 4). No dif-



ferences were found in the mean prey size of stomach and intestine and the crosstab analysis failed to find differences among the absolute frequencies. However, the intestine distribution of IU was more concentrated and the modal class was higher than the stomach classes. Thus, the smallest and the largest preys showed negative electivities in the intestine (Table 3) and the modal class (3-4mm) was the most biased (Figure 5).

Discussion and conclusions

It should be first noted that intestine supplies less dietary information than stomach since the latter contains fewer preys in the same individual. However, the high sample used here excludes this factor as the main cause of the changes found in the intestine. Nevertheless, it would be of great interest to analyse this influence in a species with relatively longer intestine than *Psammodromus hispanicus* like the herbivorous species (Carretero *et al.*, this volume and references therein, unpubl. data). However, since the origin of the preys and their sources of variation (seasonal abundance, size selection, etc.; see Díaz and Carrascal, 1990, 1993) are the same in both cases, the numbers of preys are con-

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Table 1. Comparative descriptors of the taxonomic categories found in the stomach (s), the intestine (i) and the total digestive tract (t) of *Psammotromus hispanicus*. T = total number of preys; %P = percentage of occurrence; %N = percentage of abundance; IP = Probabilistic index (' of Ruiz and Jover, 1981); IU = resource use index (Jover, 1989). Ei-s = "electivity" (Ivlev index, Ivlev 1961, modified by Jacobs, 1974) of intestine with regard to stomach.

OTU	Ts	Ti	Tt	%Ps	%Pi	%Pt	%Ns	%Ni	%Nt	IPs	IPi	IPt	IUs	IUi	IUt	Ei-s
Stylommatophora	2	0	2	0.47	0.00	0.47	0.19	0.00	0.10	0.16	0.00	0.03	0.00	0.00	0.00	0.00
Isopoda	45	3	48	10.43	1.40	10.23	4.18	0.34	2.45	4.33	0.35	2.61	3.23	0.11	1.71	-0.94
Pseudoscorpiones	13	15	28	5.21	7.01	10.70	1.21	1.70	1.43	0.68	0.75	0.59	0.79	1.30	1.11	0.25
Opiliones	16	21	37	6.16	9.81	11.16	1.49	2.38	1.89	1.77	1.87	1.39	1.09	2.05	1.55	0.31
Araneae	168	135	303	48.82	53.27	70.70	15.61	15.32	15.48	16.85	18.46	17.56	19.87	19.88	19.35	0.00
Acari	5	0	5	1.90	0.00	1.86	0.47	0.00	0.26	0.49	0.00	0.08	0.18	0.00	0.09	-1.00
Lithobiomorpha	2	3	5	0.95	0.93	1.40	0.19	0.34	0.26	0.07	0.18	0.11	0.04	0.06	0.07	0.19
Microcoryphia	14	0	14	5.69	0.00	5.58	1.30	0.00	0.72	0.90	0.00	0.37	0.88	0.00	0.44	-1.00
Dictyoptera	17	23	40	7.11	9.81	13.02	1.58	2.61	2.04	1.69	2.71	2.22	1.23	2.19	1.70	0.28
Orthoptera	45	34	79	18.01	14.95	23.26	4.18	3.86	4.04	5.27	3.85	4.58	4.32	3.72	4.07	-0.07
Dermoptera	2	3	5	0.95	1.40	2.33	0.19	0.34	0.26	0.28	0.10	0.11	0.04	0.11	0.11	0.47
Neuroptera larvae	7	12	19	3.32	4.67	7.91	0.65	1.36	0.97	0.37	0.78	0.32	0.38	0.84	0.72	0.38
Lepidoptera larvae	85	59	144	31.75	24.77	41.86	7.90	6.70	7.36	8.39	6.76	7.59	9.54	7.25	8.46	-0.14
Lepidoptera imagi	16	17	33	6.64	7.48	12.56	1.49	1.93	1.69	1.72	1.78	1.02	1.13	1.48	1.44	0.14
Diptera larvae	9	13	22	2.84	1.87	3.72	0.84	1.48	1.12	0.58	0.56	0.61	0.34	0.21	0.26	-0.24
Diptera imagi	69	40	109	22.27	17.76	30.23	6.41	4.54	5.57	6.10	3.44	4.04	6.72	4.60	5.85	-0.19
Coleoptera larvae	36	11	47	13.74	2.80	15.35	3.35	1.25	2.40	1.86	1.40	1.53	3.20	0.46	2.06	-0.75
Coleoptera imagi	115	139	254	36.49	43.93	57.21	10.69	15.78	12.98	11.47	16.08	15.21	12.41	18.98	15.23	0.21
Hymenoptera (no F)	60	45	105	16.59	16.82	28.37	5.58	5.11	5.37	5.52	3.41	3.36	3.70	4.87	4.49	0.14
Formicidae	142	122	264	24.64	23.36	34.42	13.20	13.85	13.49	12.34	13.93	15.41	12.22	10.29	11.61	-0.09
Homoptera	49	38	87	15.64	14.95	23.26	4.55	4.31	4.45	3.43	2.75	2.96	3.84	4.04	4.08	0.03
Heteroptera	153	114	267	34.12	33.18	44.19	14.22	12.94	13.64	14.29	18.35	17.31	14.77	14.24	14.06	-0.02
Ova insecta	5	0	5	1.42	0.00	1.40	0.47	0.00	0.26	0.46	0.00	0.18	0.11	0.00	0.06	-1.00
Insecta indet.	1	34	35	0.47	13.08	13.49	0.09	3.86	1.79	1.00	2.47	0.83	0.00	3.33	1.49	1.00

Fig.2 Relationships between the stomach and the intestine individual diversities of *Psammotromus hispanicus* (El Prat de Llobregat, NE Spain). $H(I)$: intestine diversity; $H(S)$: stomach diversity. The intersection point between the regression line and the line of equal diversity is marked.

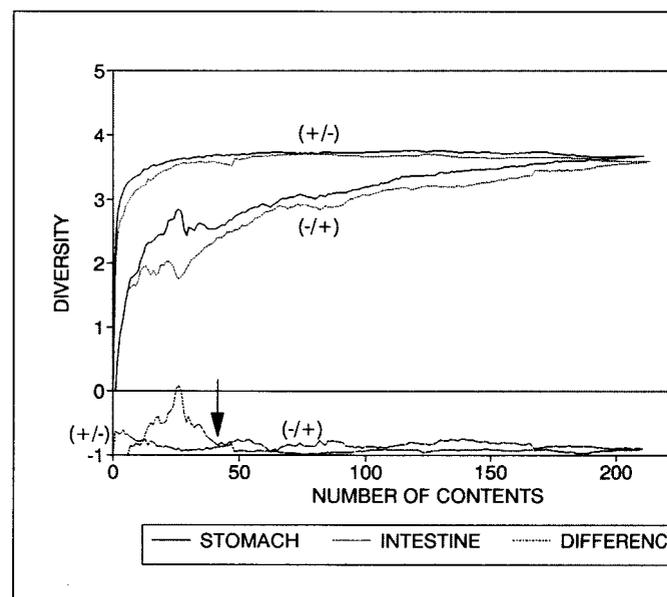
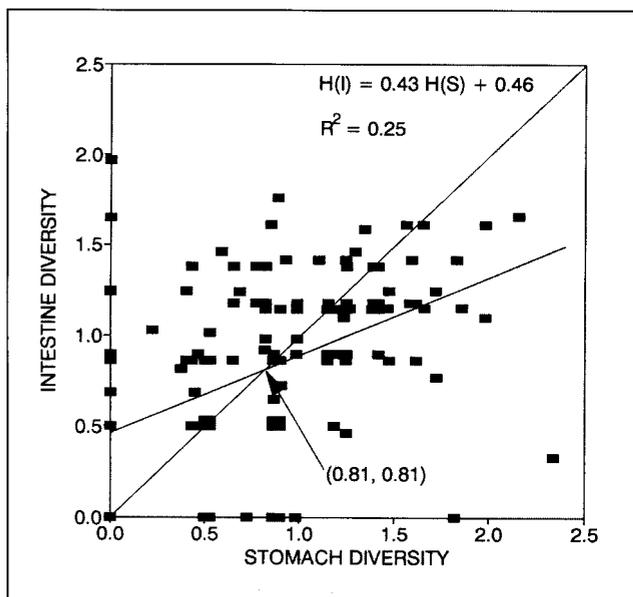


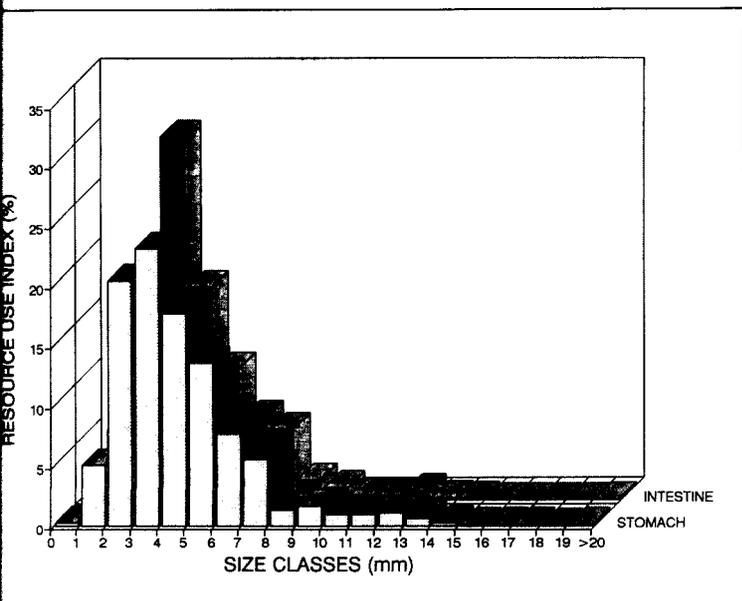
Table 2. Individual, populational and total accumulated (Hn) diversities of the taxonomic categories in the stomach, the intestine and the total digestive tract of *Psammodromus hispanicus*. N = number of contents; M = mean; S = standard deviation; SE = standard error.

Dig. portion	Individual diversity					Populational diversity				Hn
	N	M	S	CV	SE	M	S	CV	SE	
Stomach	211	0.8434	0.2528	29.97	0.0341	3.7616	0.7829	20.81	0.1056	3.67
Intestine	214	0.8209	0.1896	23.10	0.0254	3.6883	1.0436	28.29	0.1398	3.59
Total	215	1.2809	0.2659	20.76	0.0355	3.7787	0.7563	20.01	0.1011	3.71

sequently correlated.

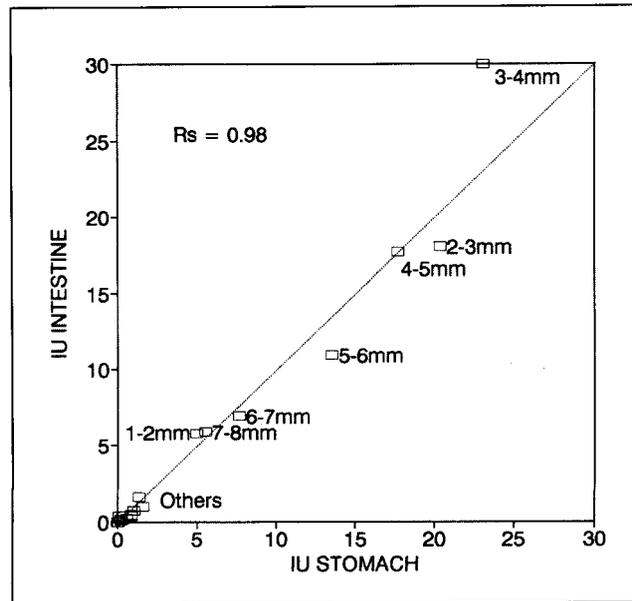
Observing the taxonomic descriptors, two kinds of effects can be observed. First, the "dietary drift" in the intestine, due to a general decrease in the identification possibilities, determines that the relative variation of a prey in the intestine depends inversely on its importance in the stomach. So, the "oligoelements"

the digestive process. This is the case of Coleoptera whose elitra persist longer than other preys allowing an easy identification even in the faecal pellets (Moreby, 1987). So, there is a paradox, since the same structures able to decrease the incidence of predation on beetles by small lacertids (Araujo, 1990, Carretero and Llorente, 1991, Grimmond *et al.*, 1994) are also responsible for their overrepresentation in the intestine. Con-



are more likely to increase, decrease or, simply, disappear from the intestine. This is the cause for the lack of four OTUs in the intestine and the extreme "electivities" of the OTUs with low resource uses.

Second, the differences in digestibility and hardness among preys (Díaz and Carrascal, 1993) can induce their misrepresentation. So, some types of prey with hard parts are especially feasible to remain until the end of



versely, some soft preys (flies, caterpillars) are less found in the intestine than in the stomach for the same reason.

The variation of trophic diversity among individuals is enormous both in the stomach and in the intestine. The intestine variance explained by the stomach is low (25%). Thus, eventual differences are difficult to register. However, it is symptomatic that intestine and

Fig. 5 Plot of the resource use (Jover, 1989) of the main preys sizes found in the stomachs and the intestines of *Psammodromus hispanicus* (El Prat de Llobregat, NE Spain).

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Table 3. Comparative descriptors of the prey sizes found in the stomach (s), the intestine (i) and the total digestive tract (t) of *Psammodromus hispanicus*. T = total number of preys; %P = percentage of occurrence; %N = percentage of abundance; IP = Probabilistic index (I' of Ruiz and Jover, 1981); IU = resource use index (Jover, 1989). Ei-s = "electivity" (lvlev index, modified by Jacobs, 1974) of intestine with regard to stomach.

Size class	Ts	Ti	Tr	%Ps	%Pi	%Pt	%Ns	%Ni	%Nt	IPs	IPi	IPt	IUs	IUi	IUt	Ei-s
0-1mm	7	4	11	2.37	1.40	2.79	0.65	0.47	0.58	1.58	0.35	0.34	0.24	0.12	0.22	-0.32
1-2mm	63	51	114	20.38	20.09	34.88	5.89	6.04	5.96	4.14	5.85	5.62	4.97	5.78	5.36	0.08
2-3mm	204	172	376	47.87	44.86	64.65	19.07	20.38	19.65	19.35	18.38	22.05	20.35	18.04	19.52	-0.06
3-4mm	225	214	439	51.18	60.28	75.35	21.03	25.36	22.94	25.77	28.69	28.91	23.05	30.28	25.59	0.14
4-5mm	184	135	319	45.97	43.46	66.05	17.20	16.00	16.67	12.37	15.29	14.24	17.70	17.69	17.25	0.00
5-6mm	131	86	217	37.44	31.78	50.70	12.24	10.19	11.34	10.52	8.50	10.51	13.53	10.90	12.40	-0.11
6-7mm	80	60	140	27.49	22.90	39.53	7.48	7.11	7.32	7.86	6.23	5.98	7.67	6.92	7.28	-0.05
7-8mm	59	52	111	22.75	20.56	34.42	5.51	6.16	5.80	4.01	7.43	4.46	5.52	5.85	5.77	0.03
8-9mm	19	18	37	8.06	8.41	14.88	1.78	2.13	1.93	3.20	2.55	1.35	1.33	1.63	1.62	0.10
9-10mm	21	15	36	9.95	5.61	14.42	1.96	1.78	1.88	0.92	1.16	0.97	1.62	0.99	1.50	-0.24
10-11mm	14	7	21	6.16	3.27	7.91	1.31	0.83	1.10	1.57	0.71	0.64	0.89	0.43	0.74	-0.35
11-12mm	14	6	20	6.16	2.80	8.37	1.31	0.71	1.05	2.39	0.34	1.07	0.89	0.34	0.73	-0.45
12-13mm	15	10	25	7.11	4.67	11.16	1.40	1.19	1.31	1.44	0.67	1.05	1.03	0.72	1.02	-0.18
13-14mm	10	4	14	4.74	1.87	6.51	0.94	0.47	0.73	0.67	1.04	0.69	0.58	0.17	0.48	-0.54
14-15mm	5	3	8	2.37	1.40	3.26	0.47	0.36	0.42	1.31	1.14	0.56	0.20	0.10	0.19	-0.33
15-16mm	3	1	4	1.42	0.47	1.86	0.28	0.12	0.21	0.15	0.04	0.08	0.08	0.00	0.07	-1.00
16-17mm	3	1	4	1.42	0.47	1.86	0.28	0.12	0.21	0.10	0.99	0.38	0.08	0.00	0.07	-1.00
17-18mm	3	0	3	1.42	0.00	1.40	0.28	0.00	0.16	1.10	0.00	0.39	0.08	0.00	0.04	-1.00
18-19mm	2	1	3	0.95	0.47	1.40	0.19	0.12	0.16	0.26	0.06	0.12	0.04	0.00	0.04	-1.00
19-20mm	1	0	1	0.47	0.00	0.47	0.09	0.00	0.05	0.11	0.00	0.02	0.00	0.00	0.00	0.00
>20mm	7	4	11	3.31	1.87	5.14	0.65	0.47	0.57	1.19	0.59	0.55	0.12	0.04	0.10	-0.47

stomach values do not increase at the same rate. In fact, individuals with euryphagous diets tend to show lower intestine diversities than expected from stomach information and vice-versa. Despite a general tendency to euryphagy (see Carretero and Llorente, 1991a), both cases are almost equally common. Really, the regression line intersects the line of equal diversity at a point with only slightly lower values than the mean diversities (see Figure 2 and Table 2). So, the intestine diversities are especially divergent for extreme values but not for intermediate ones with high data dispersion in all cases. Consequently, the stomach contents can be considered the most informative one about the trophic diversity of individuals.

The same applies to the population diversity but in a different way. The increment in the intestine variance with regard to the stomach should be interpreted as a consequence of greater heterogeneity since the rectum is emptied abruptly whereas the stomach is filled progressively. This is probably the cause of the population diversity estimation to be less precise in the intestine

than in the stomach, preventing any parametric comparison. However, there is a tendency in the intestine to underestimate the trophic diversity when values are plotted cumulatively. As mentioned by other authors (Ruiz and Jover, 1981, Ruiz, 1985, Llorente *et al.*, 1986) the +/- and -/+ ordinations represent respectively the estimations of the maximum and minimum diversity evolutions in from of content number. The study of the -/+ differences is then a conservative approach. As seen in the results, the discrepancy between intestine and stomach is especially high when the contents are less than 40.

Most of studies on the diet of Lacertidae analyse about 100-200 contents, thus sufficiently surpassing this amount. However, the samples are often divided into subgroups in order to make seasonal, sexual or age comparisons, which then reach the limits mentioned above and consequently erratic results can arise.

With regard to the size classes, the "dietary drift" is only apparent in this case because the minority preys

classes were *always* undervalued. A plausible explanation is that smallest preys are less detectable and the largest ones are systematically undermeasured. The overestimation of the modal class would then be a secondary consequence of the reduction of the percentages of the extreme classes. Conversely to the taxonomic diversity, there is here a reduction of the variation by concentration of the distribution and then the divergence between both segments is slight.

In conclusion, the intestine contains impoverished and biased dietary information in comparison with the stomach, producing an increment in the "background noise" if both are joined. This bias is larger for the taxonomic analysis than for the size one. It should be noted that only the stomach-stomach comparisons provide absolute inferences. Other homogeneous comparisons (between intestines or between total digestive tracts) would give only relative results with lower testing power but, when comparing different compartments, consequences

would be unpredictable. So, the results coming from intestine analysis should be interpreted with caution and it is recommended not to mix the two sources of information in order to describe the diet of the lizards. Since intestine is intermediate between stomach and faeces, all belonging to the same process, the stomach-faeces divergence should be greater than that found here but following the same tendency. This seems to be the case of the results reported by Seva (1982) for the lacertid *Acanthodactylus erythrurus*. Moreover, in the case of low sample sizes, if the intestine and stomach data have to be mixed it is recommended (against the usual procedure) to exclude the rectum because it is the most biased part of the digestive tract. As a consequence of these findings, it can be also predicted that the more OTUs or prey sizes are consumed, the more easily intradigestive differences appear and vice-versa. So, the lacertids with generalist trophic strategies and large body sizes are more liable to show these undesirable effects.

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