

Digestive size and diet in Lacertidae: a preliminary analysis

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Introduction

Several morphological specializations of the digestive tract in relation with herbivory have been described in a number of lizards, mainly Iguanidae (OSTROM 1963, MCBEE 1971, NAGY 1977, JOHNSON & LILLYWHITE 1979, MCBEE & MCBEE 1982, CHRISTIAN et al. 1984, TROYER 1984). Large iguanas often show enlarged intestines and compartmentalized colons (IVERSON 1980, 1982). Other small lizards belonging to the family Teiidae have only been reported to increase the intestine capacity in the insular, herbivorous forms but not in the entomophagous ones (DEARING 1993). Although such variations have been assumed to occur also in other families (see previous references), they have seldom been demonstrated. Some members of the family Lacertidae have shifted from a primarily entomophagous diet to herbivory (see for instance, PÉREZ-MELLADO & CORTI 1993). Nevertheless, with the exception of the large species belonging to the Canarian genus *Gallotia* (LLORENTE pers. com.), the rest are small lizards which seem to lack any specific anatomical features for herbivory. It has been proposed that the increase of the gut capacity (and length) and, consequently, the retention time of the food may be an adaptation for eating low profitable preys, mainly plant matter (DEARING 1993). However, other factors also could be involved.

This paper is a first approach to testing this hypothesis in several populations of small-sized lacertid species whose diet has been previously analyzed. Thus, the degree of inter- and intraspecific variation of digestive capacity is analyzed.

Material and methods

989 specimens of all sizes belonging to five species of small lacertids were captured throughout the period of activity in different localities of NE Spain as a part of different studies on trophic ecology (see tab. 1). Animals were sacrificed humanely, injected with and stored in 70 % ethanol. Since the storage period before measurements was very similar (2 - 3 years, from 1992 to 1995 for *Podarcis pityusensis* and from 1986-87 to 1989 in the remaining species and populations), the consequent decrease in elasticity (VITT et al. 1985) was assumed to be uniform in all cases. At the laboratory, the snout-vent length (SVL) was measured and, after dissection, the complete digestive tract was extracted. Then, the length

and width of the stomach and the intestine were measured. In order to make the measurements uniform, each organ was stretched to its maximum length without disturbing the integrity of the tissue (DEARING 1993). All measures were taken with a caliper to the nearest 0.05 mm. The stomach and intestine capacities were calculated, supposing them to be ellipsoidal and cylindrical, respectively, by using the following formulae:

$$C_s = \frac{4}{3} \pi \frac{a}{2} \left(\frac{b}{2}\right)^2 \quad C_i = \pi \left(\frac{a}{2}\right)^2 b$$

where C_s and C_i are the stomach and intestine capacities, respectively, and a is the width and b is the length of each organ.

Species	Locality	UTM	Cap. dates	Diet	Reference
<i>Acanthodactylus erythrurus</i>	Torredembarra	31TCF6857	1986-87	entom.	CARRETERO (1993)
<i>Acanthodactylus erythrurus</i>	Ebro Delta	31TCF1810	1986-87	entom.	CARRETERO & LLORENTE (1993)
<i>Psammodromus algirus</i>	Aiguamolls de l'Empordà	31TEG1075/ 0975/0974	1986-87	entom.	CARRETERO & LLORENTE (1993)
<i>Psammodromus algirus</i>	Torredembarra	31TCF6857	1986-87	entom.	CARRETERO (1993)
<i>Psammodromus algirus</i>	Ebro Delta	31TCF1810	1986-87	entom.	CARRETERO & LLORENTE (1993)
<i>Psammodromus hispanicus</i>	El Prat de Llobregat	31TDF2370	1986-87	entom.	CARRETERO & LLORENTE (1991)
<i>Podarcis hispanica</i>	Torredembarra	31TCF6857	1986-87	entom.	CARRETERO (1993)
<i>Podarcis pityusensis</i>	Barcelona	31TDF3384	1992	partly herbiv.	CARRETERO et al. (1995)

Tab. 1. Species, localities and general diet of the lacertids analyzed in this study.

Analysis of covariances, ANCOVA (SOKAL & ROHLF 1981), was used to compare the values of digestive capacity (and length) among groups, standardizing the effect of body size. After log-transformation of the variables, the relative capacity of each digestive portion was calculated as the standard residual of the absolute capacity using lizard SVL as covariate.

Results

All the lacertids analyzed lacked any compartmentalization of the intestine and the observed variations were limited to the relative size of the digestive organs. The correlations and the regression lines between the digestive capacities and the body size are shown in table 2. Digestive capacity increased exponentially with body size. In all cases, the slopes of the stomach capacity-body size lines were lower than those of the intestine capacity-body size (both log-transformed, tests of parallelism, $p < 0.01$). The slopes of the total digestive capacity-body size reached intermediate values. The intestine length also increased exponentially since all the slopes were significantly different from 1 (tests of parallelism, $p < 0.01$).

The relative stomach capacities (tab. 3) were different among populations (ANCOVA, $F = 8.103$; 7, 980 d.f.; $p = 4.37 \cdot 10^{-9}$, for the adjusted means, no slope differences). Post hoc tests (tab. 4) revealed no variation among the populations of the same species. *P. pityusensis* and *Acanthodactylus erythrurus* were the species with the largest stomachs and no differences between them were found. *Psammodromus algirus* and *Podarcis hispanica* showed intermediate stomach sizes and, finally, *Psammodromus hispanicus* showed lower values than the others.

The intestine capacities (ANCOVA, $F = 6.717$; 7, 980 d.f.; $p = 1.80 \cdot 10^{-7}$), the total digestive capacities (ANCOVA, $F = 7.187$; 7, 980 d.f.; $p = 5.08 \cdot 10^{-6}$) and the intestine lengths (ANCOVA, $F = 20.01$; 7, 980 d.f.; $p = 6.52 \cdot 10^{-22}$) were also significantly different among species. Results similar to those of the stomachs were found for post hoc tests (tabs. 4 and 5). However, the slopes were also different between species for the three variables (ANCOVAs, $F = 4.789$; 7, 973 d.f.; $p = 3.39 \cdot 10^{-5}$; $F = 2.564$; 7, 973 d.f.; $p = 0.0012$; $F = 13.769$; 7, 973 d.f.; $p = 2.03 \cdot 10^{-15}$). In fact, the slopes of these regression lines were again higher in *P. pityusensis* and *A. erythrurus* than in the rest of the species, and especially low in *P. hispanica* (see tab. 2).

Species	Locality	N	R ²	regression line
<i>A. erythrurus</i>	Torredembarra	68	0.85	Cs = 0.0204 SVL ^{2.81}
		68	0.81	Ci = $3.8 \cdot 10^{-5}$ SVL ^{3.56}
		68	0.85	Ct = 0.0195 SVL ^{2.83}
		68	0.87	Li = 1.71 SVL - 16.25
<i>A. erythrurus</i>	Ebro Delta	87	0.79	Cs = 0.0079 SVL ^{3.01}
		87	0.88	Ci = $1.6 \cdot 10^{-7}$ SVL ^{4.83}
		87	0.80	Ct = 0.0066 SVL ^{3.07}
		87	0.90	Li = 1.91 SVL - 28.42
<i>P. algirus</i>	Aiguamolls E.	141	0.82	Cs = 0.0178 SVL ^{2.80}
		141	0.82	Ci = $1.7 \cdot 10^{-5}$ SVL ^{3.73}
		141	0.82	Ct = 0.0162 SVL ^{2.84}
		141	0.88	Li = 1.36 SVL - 5.88
<i>P. algirus</i>	Torredembarra	156	0.81	Cs = 0.0072 SVL ^{3.07}
		156	0.86	Ci = 10^{-5} SVL ^{3.86}
		156	0.81	Ct = 0.0068 SVL ^{3.09}
		156	0.89	Li = 1.41 SVL - 7.50
<i>P. algirus</i>	Ebro Delta	133	0.80	Cs = 0.0038 SVL ^{3.19}
		133	0.86	Ci = $3.6 \cdot 10^{-6}$ SVL ^{4.09}
		133	0.82	Ct = 0.0035 SVL ^{3.23}
		133	0.90	Li = 1.44 SVL - 8.65
<i>P. hispanica</i>	El Prat de Ll.	215	0.54	Cs = 0.0162 SVL ^{2.82}
		215	0.53	Ci = $6.5 \cdot 10^{-5}$ SVL ^{3.40}
		215	0.56	Ct = 0.0158 SVL ^{2.84}
		215	0.62	Li = 1.19 SVL - 4.29
<i>P. hispanica</i>	Torredembarra	44	0.65	Cs = 0.0224 SVL ^{2.75}
		44	0.54	Ci = 0.0001 SVL ^{3.26}
		44	0.66	Ct = 0.0219 SVL ^{2.77}
		44	0.73	Li = 1.46 SVL - 11.24
<i>P. pityusensis</i>	Barcelona	145	0.76	Cs = 0.001 SVL ^{3.49}
		145	0.56	Ci = $9.8 \cdot 10^{-7}$ SVL ^{4.45}
		145	0.77	Ct = 0.0009 SVL ^{3.53}
		145	0.72	Li = 1.66 SVL - 19.87

Tab. 2. Correlations and regression lines between the stomach (Cs), intestine (Ci) and total digestive (Ct) capacities and the intestine length (Li) with the body size (SVL) in the lacertids analyzed. All the correlations were significant ($p < 0.01$).

Species	Locality	Cs	Ci	Ct	Li
<i>A. erythrurus</i>	Torredembarra	2.9782 (0.0231)	1.4883 (0.0311)	3.1091 (0.0225)	67.0531 (0.9946)
<i>A. erythrurus</i>	Ebro Delta	2.9182 (0.0206)	1.3295 (0.0277)	3.1077 (0.0200)	66.1840 (0.8871)
<i>P. algirus</i>	Aiguamolls E.	2.9136 (0.0160)	1.4409 (0.0216)	2.9491 (0.0156)	59.4385 (0.6881)
<i>P. algirus</i>	Torredembarra	2.9678 (0.0152)	1.4249 (0.0205)	2.9467 (0.0148)	60.4486 (0.6540)
<i>P. algirus</i>	Ebro Delta	2.9001 (0.0165)	1.3684 (0.0222)	2.9427 (0.0160)	60.4363 (0.7082)
<i>P. hispanicus</i>	El Prat de Ll.	2.9218 (0.0136)	1.5172 (0.0183)	2.7069 (0.0132)	55.8696 (0.5883)
<i>P. hispanica</i>	Torredembarra	2.9382 (0.0287)	1.4776 (0.0387)	2.8482 (0.0279)	59.5366 (1.2353)
<i>P. pityusensis</i>	Barcelona	2.8185 (0.0162)	1.4448 (0.0218)	3.0628 (0.0158)	61.2411 (0.6964)

Tab. 3. Mean relative capacities of the stomach (Cs), the intestine (Ci) and the total digestive tract (Ct) and mean relative length (Li) of the lacertids analyzed (capacities are log-transformed). Standard deviations are in parentheses.

Cs\Ci	AE(Tor.)	AE(Ebro)	PA(Aig.)	PA(Tor.)	PA(Ebro)	Psh(Prat)	PH(Tor.)	PP(Bar.)
AE(Tor.)	-	n.s.	*	*	*	*	*	n.s.
AE(Ebro)	n.s.	-	n.s.	*	*	*	*	*
PA(Aig.)	*	*	-	n.s.	n.s.	*	n.s.	*
PA(Tor.)	*	*	n.s.	-	n.s.	*	n.s.	*
PA(Ebro)	*	*	n.s.	n.s.	-	*	n.s.	*
Psh(Prat)	*	*	*	*	*	-	n.s.	*
PH(Tor.)	*	*	n.s.	n.s.	n.s.	*	-	*
PP(Bar.)	n.s.	n.s.	*	*	*	*	*	-

Tab. 4. Results of the Scheffé's post hoc tests performed after significant ANCOVAs. Groups were analyzed for the values of the stomach (Cs) and the intestine (Ci) capacities using the body size (SVL) as covariate (variables log-transformed). Cs: symbols below the diagonal; Ci: symbols above the diagonal; * significant $p < 0.01$; n.s. not significant. AE = *Acanthodactylus erythrurus*, PA = *Psammodromus algirus*, PSH = *Psammodromus hispanicus*, PH = *Podarcis hispanica*; PP = *Podarcis pityusensis*.

Ct\Li	AE(Tor.)	AE(Ebro)	PA(Aig.)	PA(Tor.)	PA(Ebro)	Psh(Prat)	PH(Tor.)	PP(Bar.)
AE(Tor.)	-	n.s.	*	*	*	*	*	*
AE(Ebro)	n.s.	-	*	*	*	*	*	*
PA(Aig.)	*	n.s.	-	n.s.	n.s.	*	n.s.	*
PA(Tor.)	*	*	n.s.	-	n.s.	*	n.s.	*
PA(Ebro)	*	*	n.s.	n.s.	-	*	n.s.	*
Psh(Prat)	*	*	*	*	*	-	*	*
PH(Tor.)	*	*	n.s.	n.s.	n.s.	n.s.	-	n.s.
PP(Bar.)	n.s.	*	*	*	*	*	*	-

Tab. 5. Results of the Scheffé's post hoc tests performed after significant ANCOVAs. Groups were analyzed for the values of the total digestive capacity (Ct) and the intestine length (Li) using the body size (SVL) as covariate (Ct log-transformed). Ct: symbols below the diagonal; Li: symbols above the diagonal; * significant $p < 0.01$; n.s. not significant. AE = *Acanthodactylus erythrurus*, PA = *Psammodromus algirus*, PSH = *Psammodromus hispanicus*, PH = *Podarcis hispanica*; PP = *Podarcis pityusensis*.

Discussion and conclusions

The results point out the relevance of the digestive size as a morphological feature in the lacertids analyzed. The variations of these traits are not random since they remain relatively stable within the species limits and they show consistent differences among species (see results). However, especialization for herbivory cannot solely explain the digestive patterns observed.

First of all, the geometrical constraints of the digestive dimensions in the abdominal cavity of a lizard should be taken into account. A tridimensional measure must increase exponentially with a linear one in the same animal (SOKAL & ROHLF 1981). Consequently, results indicate that small lizards carry relative smaller digestive organs than big ones. In the same way, the length of the intestine also showed positive allometry with regard to body size because the larger the abdominal cavity, the more intestinal loops can be contained. Since immature lizards have relatively smaller and shorter digestive tracts, the retention time and biomass of the food stored would be lower. This could prevent small lizards from eating food with low digestibility and especially plant matter. In fact, this phenomenon has been registered in lizards at different size scales (POUGH 1973, CARRETERO et al. in press). However, it cannot be considered an adaptation but a result of an anatomical constraint, and only the behaviour of immatures avoiding the consumption of low profitable preys may be adaptative. Nevertheless, although all the species followed the same allometric pattern, interspecific differences were found, even between species of the same genus.

The stomach capacity indicates the possibility of storing and digesting a certain amount of food throughout a hunting day (SEVA 1982), the intestine capacity would determine the food amount liable to post-gastric digestion, and the intestine length would be an estimator of the duration of this process (CHRISTIAN et al. 1984, JOHNSON & LILLYWHITE 1979). The results point out that the three variables have coevolved since the differences among species are constant for all of them. In fact, the consumption of low profitable prey should induce lizards to develop large stomachs storing great amount of biomass and large, elongated intestines allowing the fermentative flora to carry out their mission. Nevertheless, the rates of stomach increase are always the same whereas the intestine rates vary among species in the same way as the main relative values. This fact could imply that natural selection would act mainly on the intestinal segment. Moreover, factors other than the energy input, such as historical constraints and energetic costs associated with predation (DÍAZ & CARRASCAL 1993) should be taken into account.

P. pityusensis is an omnivorous, insular species consuming a considerable percentage of plant matter and heavily chitinized insects, all energetically defective (PÉREZ-MELLADO & CORTI 1993, DÍAZ & CARRASCAL 1993, CARRETERO et al. 1993). This tactic remains partially fixed even after the translocation to the continent, which is the case of the population studied (see CARRETERO et al. in press). So, it is not strange to find large digestive organs in this species in comparison to the continental and strictly entomophagous *P. hispanica* which feeds mainly on spiders (CARRETERO 1993), a soft and profitable prey (DÍAZ & CARRASCAL 1993).

A. erythrurus belongs to an apomorphic lineage of Lacertidae (ARNOLD 1989) which evolved under desert conditions (ARNOLD 1983, 1984) and shows a tendency to myrmecophagy (ARNOLD 1984, PÉREZ-MELLADO 1992). Although *A. erythrurus* is an extreme species wit-

hin its genus (GIL et al. 1993) and the populations of NE Spain eat fewer ants than others (see CARRETERO 1993, CARRETERO & LLORENTE 1993 and references therein), the general features of the genus persist indicating the importance of the historical constraints. These include the robustness of the trunk, which is thus able to contain the relative larger digestive apparatus. An adaptive explanation would link diet and morphology. However, as indicated by ARNOLD (1993), the selective pressures which promoted the robust body shape are not necessarily the same as those that operate at present and other factors (for instance egg or fat allocation, CARRETERO & LLORENTE 1995) could be implied.

Finally, the *Psammodromus* species of NE Spain are characterized by a very diverse diet which consists only of Arthropoda, with a low proportion of Formicidae (see CARRETERO 1993). So, this could be related with the relatively small stomach and intestine found, especially in the small *P. hispanicus*. This is also the case of *Podarcis hispanica*. Nevertheless, it should be considered that both genera are also plesiomorphic within the family Lacertidae (ARNOLD 1989).

The present study is only a first step in the analysis of the digestive size variation in Lacertidae. Further research should discriminate ecological from historical effects on digestive size: more species belonging to homogeneous groups (preferably genera) and with heterogeneous diets should be investigated; the largest species should also be studied in order to determine the extreme size effects; and, finally, the most differentiated lineages with clear trophic specializations should be analyzed in search of macroevolutionary changes affecting the digestive tract.

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