USE OF FAECAL AND STOMACH CONTENTS IN ASSESSING FOOD NICHE RELATIONSHIPS: A CASE STUDY OF TWO SYMPATRIC SPECIES OF *PODARCIS* LIZARDS (SAURIA: LACERTIDAE)

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RÉSUMÉ

La niche trophique de deux espèces de lézards (*Podarcis muralis* et *P. sicula*) a été étudiée en analysant à la fois des contenus stomacaux et des pelotes fécales. Des comparaisons ont été conduites entre les deux espèces, portant sur leurs spectres trophiques, les largeurs et les recouvrements de leurs niches alimentaires. L'analyse fondée sur les contenus stomacaux a fourni les données les plus complètes et les plus détaillées. *Podarcis sicula* est apparu comme un prédateur plus généraliste que *P. muralis,* le recouvrement de niche entre ces deux espèces étant très faible. Les données différentes qui existent dans la littérature, montrant un plus fort recouvrement, seraient dues à des préférences alimentaires locales et à l'utilisation de méthodes d'analyse différentes.

SUMMARY

The trophic niche of two sympatric species of wall lizards (*Podarcis muralis* and *P. sicula*) was studied by the analysis of both stomach contents and faecal pellets, and differences in trophic spectra, food niche breadth, and niche overlap were compared. The analysis based on stomach contents provided more complete and detailed data. *Podarcis sicula* appeared to be a more generalist predator than *P. muralis,* and the niche overlap between the two species was very low. Differences from literature data showing a higher overlap can be due to local food preferences and different methods of analysis.

INTRODUCTION

The trophic niche is one of the most relevant aspects in the study of animal autoecology and represents an important approach in understanding the ecological relationships among species in a community. For these reasons, during a more comprehensive research (Bombi & Bologna, unpublished data) on the competition between *Podarcis sicula,* an Italian sub-endemic element, known for his adaptability particularly to open habitats, and *Podarcis muralis,* a South-European species common in several kind of habitats, particularly in bush, forest and rocky

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ones, particular attention was paid to study the trophic niche of these species. The distribution and ecology of these species at regional level (Latium) were recently analysed by Bologna *et al.* (2000). *Podarcis* is a genus morphologically and ecologically very homogeneous (Böhme, 1986), recently revised from a biogeographical and phylogenetical point of view by Oliverio *et al.* (2000).

Several techniques were tested to study the feeding habits of lizards. The dissection of specimens collected and killed (*e.g.*, Pollo & Pérez-Mellado, 1988; Pérez-Mellado, 1992), or already preserved in museums (*e.g.*, Pérez-Mellado & Corti, 1993), is the most efficient method, but now this procedure is more rarely adopted to reduce the drawing of specimens from the field. Two other techniques, the faecal pellets analysis (FPA) and the stomach flushing (SF), were frequently used. Thanks to its innocuity and facility of use (Angelici *et al.*, 1997), FPA is a favoured method in researches on lizard diet (*e.g.*, Capula *et al.*, 1993; Capula & Luiselli, 1994; Rugiero, 1994; Hódar *et al.*, 1996; Capizzi, 1999). The SF method, proposed by Legler (1977) for freshwater turtles, is another innocuous but quite laborious technique which permits to draw the ingested food components before the digestive processes. This method, largely used for other vertebrates, has been rarely applied to lizards (*e.g.*, Legler & Sullivan, 1979; James, 1990). Some authors have recently proposed various innocuous and poorly invasive methods also for reptiles. For example, Rivas *et al.* (1996) proposed to fill the stomach with water, holding vertically the animal with the head up in position, and then removing the stomach contents by inverting the lizard position. By contrast, Luiselli *et al.* (1998) obtained the ingested prey of snakes by gentle palpation of the animal abdomen. However, such techniques, sometimes difficult to apply, have not been widely adopted. There are only few papers dealing with the feeding habits of the genus *Podarcis* (*e.g.*, Sorci, 1990; Capula *et al.*, 1993; Pérez-Mellado & Corti, 1993; Capula & Luiselli, 1994; Rugiero, 1994) but only a few using the SF method (*e.g.*, Richard & Lapini, 1993).

The aims of this work are: (a) to describe the feeding habits of *P. sicula* and *P. muralis* in an area of sympatry, where a possible case of competitive interaction has been noted (Bombi & Bologna, unpublished data); (b) to compare the efficiency of the FPA and SF methods.

MATERIALS AND METHODS

STUDY AREA

The research was carried out in southern Latium (Central Italy, Latina and Frosinone provinces), within an area approximately included between 41° 12' N and 41° 27' N, and between 12° 54' E and 13° 54' E.

The bioclimate and vegetation are typically Mediterranean along the Thyrrhenian coasts, while they are usually more mesic in the mountain areas (Blasi, 1994). The main vegetation types occurring in the study area include: (a) scrubs and woodlands, respectively dominated by evergreen (*Quercus ilex* and *Q. suber*) or dedicuous (*Q. pubescens*) oaks, along the coasts; (b) mesic woodlands dominated by various deciduous species (*e.g., Fagus sylvatica, Quercus cerris* and *Ostrya carpinifolia*) in mountain areas; (c) steppic habitats dominated by *Ampelodesmos mauritanicum* on the xeric mountain slopes.

Sixty two sampling sites of this area, from sea level to 900 m a.s.l., were visited during 34 days of observation, approximately weekly distributed from 13 March 1999 to 26 October 1999.

Both *P. sicula* and *P. muralis* occur in this area. The local population of *P. sicula* is represented by two subspecies, *campestris* and *sicula,* with a possible area of introgression, whereas that of *P. muralis* is currently referred to the ssp. *nigriventris.*

TECHNIQUES ADOPTED

The FPA consisted in the collection of faeces given out by lizards when captured, or just later. This technique needs just a few seconds and a very simple equipment (a plastic vial), but the lizards sometimes do not defecate immediately after capture.

The SF method proposed by Legler & Sullivan (1979) consists in the introduction of water in the animal stomach by a plastic tube connected to a syringe, and in the collection of stomach contents washed out. The SF method adopted for the present study, includes some minor changes to make it simpler and less invasive: (a) the complicated device of pumping was replaced by a simpler and less expensive big enema; (b) the dangerous intravenous catheter was replaced by a safer urological one (Nelaton Orlycatnel, $\Phi = 3$ mm) having the exit holes laterally in position, thus extremely reducing the risks of damages to the gastric mucosa; (c) the plastic ring, used to keep open the lizard mouth, was supplied with a short thread which, attached to a worker finger, helps to maintain the ring in position. All this procedure needs approximately 15 minutes for every specimen to be used.

Prey items were preserved in ethanol alcohol (70 %) and identified to the more detailed taxonomic level, with the assistance of specialists of different taxa (see Acknowledgements).

DATA ANALYSIS

Data obtained by both techniques were independently used to describe the trophic niche of the wall lizard species, to identify the most preyed taxa, and to calculate indices of niche diversity and overlap. In order to estimate the euriphagy of the species, both Shannon & Wiener and Simpson diversity indices were used. The *t*-test on the weekly values of this indices were used to assess the statistical significance of the differences. Both Pianka and Morisita overlap indices were used to calculate the trophic niche overlap of the two species. These indices were also applied to the data obtained for the same species using the FPA and SF methods to evaluate their consistence. The trophic spectra of the species were compared using χ^2-test by two contingency tables (FPA of *P. sicula vs.* FPA of *P. muralis*; SF of *P. sicula vs.* SF of *P. muralis*). The same analysis was carried out on trophic spectra of each species derived by both techniques utilised (FPA of *P. sicula vs.* SF of *P. sicula*; FPA of *P. muralis vs.* SF of *P. muralis*).

The number of identified taxa and specimens for different taxonomic levels, and the frequency of the identified specimens in each level were calculated by using both faeces and stomach contents. To define the value of techniques in the examination of the trophic niches, both methods were analysed and compared using different taxonomic levels of identification.

RESULTS

We analysed 25 faecal pellets (113 prey items) and 51 stomach contents (225 prey items) of *P. sicula,* and 8 faecal pellets (43 prey items) and 12 stomach contents (29 prey items) of *P. muralis*. The prey items were identified to various detailed taxonomic levels (Table I).

TABLE I

Taxonomic identification levels of prey items obtained by FPA and SF methods: n = number of prey individuals identified to each taxonomic level; f = frequency of prey individuals identified to each taxonomic level.

			Phylum	Class	Order	Suborder	Family	Subfamily	Genus	Species	Total
	FPA	n	6	27	43	3	10	3	3	18	113
P. sicula		f	0.053	0.239	0.381	0.027	0.088	0.027	0.027	0.159	1
	SF	n	4	28	63	13	33	3	49	32	225
		f	0.018	0.124	0.280	0.058	0.147	0.013	0.218	0.142	1
	FPA	n	0	25	11	0	2	0	3	2	43
P. muralis		f	0.000	0.581	0.256	0.000	0.047	0.000	0.070	0.047	1
	SF	n	1	5	15	3	2	0	3	0	29
		f	0.034	0.172	0.517	0.103	0.069	0.000	0.103	0.000	1

The number of preys analysed is greater than in every other previous study on *P. sicula* and *P. muralis,* and extremely more detailed in the taxonomical level of identification (Appendix). The dominant taxa obtained are the Hymenoptera (particularly Formicidae) and Hemiptera for *P. sicula*; Arachnida (particularly Opiliones) and Orthoptera for *P. muralis*. The Nematoda present only in the *P. sicula* faeces could be only endoparasites.

An analysis of the levels of taxonomic identification which were obtained by using the FPA and SF methods (Table I) shows that the SF method provides more accurate data, since a higher number of prey items and taxa were identified to a more detailed taxonomic level, using this technique.

The diversity indices are apparently higher in *P. sicula* than in *P. muralis* and in SF than FPA (Table II), nevertheless a *t*-test for the weekly values of the diversity indices shows not significant differences between the two species as well as between the two methods.

The niche overlap of the two species shows a low degree of food overlap if their diets are assessed by the SF method, while the FPA strongly overestimate their niche overlap (Table III). The detailed identification and the selectivity of the SF method, produce a reduction of significance of the differences. Consequently it increases the indices of overlap, calculated using the data emerging by FPA (Table III).

TABLE II

Diversity indices of the trophic spectra obtained from both FPA and SF.

	FPA		SF	
	P. sicula	*P. muralis*	*P. sicula*	*P. muralis*
Simpson	11.556	3.959	19.783	10.922
Shannon-Wiener	2.923	1.854	3.604	2.612

TABLE III

Values of food niche overlap (calculated by means of Pianka and Morisita indices) between P. sicula *and* P. muralis *using data obtained by FPA and SF methods and between diets obtained by FPA and SF methods in the two* Podarcis *species.*

	FPA *vs.* SF		*P. sicula vs. P. muralis*	
	P. sicula	*P. muralis*	FPA	SF
Pianka	0.657	0.491	0.813	0.442
Morisita	0.615	0.405	0.685	0.420

Highly significant differences in taxonomic composition of trophic spectra (tested by χ^2-test, calculated by four contingency tables) were found between the two species, as well as within each species according to the method (Table IV).

TABLE IV

Results of χ^2-test (calculated by four contingency tables) between the trophic spectra of P. sicula *and* P. muralis *using data obtained by FPA and SF methods, and between diets obtained by FPA and SF methods in the two* Podarcis *species.*

	FPA *vs.* SF		*P. sicula vs. P. muralis*	
	P. sicula	*P. muralis*	FPA	SF
χ^2	49.67	20.95	22.39	57.62
df	13	4	7	6
P	< 0.01	< 0.01	<0.01	< 0.01

The low value of the indices of overlap between diets obtained from FPA and SF contents (Table III), and the differences between the taxonomic compositions of diets obtained from FPA and SF contents (Table IV), confirm that the two different techniques describe differently the same trophic niche. Moreover, the overlap between the two species obtained using the data of SF showed a low value.

DISCUSSION

Based on our results the SF method appears to be the most efficient bloodless technique to study the trophic niche of lizards. The relative laboriousness of the procedure is greatly rewarded by the higher detail in prey identification and by the completeness of the obtained samples. This can be due to the fact that the specimens are less damaged in the stomach contents than in faeces, particularly only some taxa with well sclerotized or calcified anatomical parts can be easily identified in faeces. Such effects of the digestive processes on prey identification could introduce serious biases in assessing feeding habits. In particular, as some prey items are less affected than others by digestion, their higher occurrence in faeces could be erroneously regarded as a predator preference for such prey. For example, the FPA method hid the selective preference of *P. muralis* for arachnids or the relevant presence of butterflies in the diet of *P. sicula*. Consequently, the SF technique is advisable if the death of the specimen must be avoided and a relative higher effort of research can be lavished.

As to the feeding ecology of the two *Podarcis* species analysed here, the SF method allowed us to assess that the differences between the food habits of these two species can be found in the detailed taxonomical compositions of their trophic niche and not in the synthetic indices of diversity. It allowed also to describe *P. sicula* as a predator with a certain predilection for ants, but also eating a number of other invertebrates like bugs and moths (Appendix 1). By contrast, using the same techniques, *P. muralis* appears as a predator feeding in preference on Arachnida, notably harvestmen (Appendix 1).

Such differences in the alimentary habits of these species, also proved by low values of overlap indices (Table III), have a double interest. From an autoecological point of view, these differences can suggest a preference of *P. sicula* for open and warm habitats (typical for ants) and a preference of *P. muralis* for wood and rocky habitats (typical for sciaphylous and hygrophylic harvestmen). From a synecological point of view, these differences can clarify how two similar species can be syntopic and reduce interspecific competition for trophic resources.

Our results greatly differ from those obtained by other researches on *P. sicula* and *P. muralis* using different methods (*e.g.*, Capula *et al.*, 1993; Pérez-Mellado & Corti, 1993; Rugiero, 1994). Such differences concern both food spectra and values of breadth and overlap of trophic niches. The food niche we observed is larger in both species while the overlap indices are evidently reduced. Capula *et al.* (1993) interpreted their results as a consequence of the species assemblage organization based on the ecological needs of each species, rather than by species interactions. By contrast the low value of overlap between the food niches, and the fairly differentiated trophic spectra observed in our study, suggest that competitive interactions among the species of such a guild would be of great importance in moulding their ecological role in a natural community.

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APPENDIX

List of the food items obtained from FPA and SF methods of P. sicula *and* P. muralis. *Nomenclature and taxonomical order follow Minelli* et al. *(1993-1995).*

	FPA				SF			
	P. sicula		*P. muralis*		*P. sicula*		*P. muralis*	
	n	f	n	f	n	f	n	f
Nematoda ind.	4	0.035						
Gastropoda ind.	1	0.009			5	0.022	1	0.034
Dysdera erythrina (Dysderidae)					1			
Drassodes sp. (Gnaphosidae)					1			
Zelotes sp. (Gnaphosidae)					1			
Philodromus sp. (Philodromidae)					1			
Lycosidae ind.					1			
Salticidae ind.					1			
Araneae ind.	7		3		3		4	
Araneae tot.	7	0.062	3	0.070	9	0.040	4	0.138
Phalangiidae ind.					1			
Opiliones ind.							6	
Opiliones tot.	0	0.000	0	0.000	1	0.004	6	0.207
Parasitiformes ind.					1			
Acari ind.					3			
Acari tot.	0	0.000	0	0.000	4	0.018	0	0.000
Arachnida ind.			3		2			
Arachnida tot.	7	0.062	6	0.140	16	0.071	10	0.345
Trichoniscus sp. (Trichoniscidae)							1	
Isopoda ind.	1				1		1	
Isopoda tot.	1	0.009	0	0.000	1	0.004	2	0.069
Pachymerium ferrugineum (Geophilidae)					1			
Eupolybothrus sp. (Lithobiidae)					1			
Lithobiidae ind.	1							
Chilopoda tot.	1	0.009	0	0.000	2	0.009	0	0.000
Julinae ind. (Julidae-Diplopoda)					1	0.004		
Blattaria ind.	2	0.018			7	0.031		
Celifera ind.					4		2	
Ensifera ind.					1			
Orthoptera ind.	6		2		9		1	
Orthoptera tot.	6	0.053	2	0.047	14	0.062	3	0.103
Scutelleridae ind.					1			
Nabidae ind.					1			

	FPA				SF			
	P. sicula		*P. muralis*		*P. sicula*		*P. muralis*	
	n	f	n	f	n	f	n	f
Pentatomidae ind.					1			
Heteroptera ind.	2				4			
Aphididae ind.					4			
Cicadidae ind.					1			
Homoptera ind.					1			
Hemiptera ind.	15		1		11		2	
Hemiptera tot.	17	0.150	1	0.023	24	0.107	2	0.069
Trichoptera ind.					1	0.004		
Lymantria dispar (Lymantriidae)					1			
Geometridae ind.					1			
Psichidae ind.					1			
Lepidoptera ind.					18		1	
Lepidoptera tot.	0	0.000	0	0.000	21	0.093	1	0.034
Aphaenogaster senilis (Formicidae)	12				10			
Camponotus aethiops (Formicidae)	1				1			
Camponotus fallax (Formicidae)					4			
Camponotus piceus (Formicidae)					1			
Crematogaster sordidula (Formicidae)	1							
Crematogaster scutellaris (Formicidae)			2					
Linepithema humile (Formicidae)					1			
Pheidole pallidula (Formicidae)	4				7			
Formica sp. *fusca* group (Formicidae)							1	
Diplorhoptrum sp. (Formicidae)	1				36			
Leptothorax sp. (Formicidae)			3				1	
Messor sp. (Formicidae)	1				7			
Myrmica sp. (Formicidae)					1			
Formicinae ind. (Formicidae)	1							
Myrmicinae ind. (Formicidae)					1			
Formicidae ind.	5		1		2			
Formicidae tot.	26	0.230	6	0.140	71	0.316	2	0.069
Chrysididae ind.	1							
Diapriidae ind.					1			
Sphecidae ind.					1			
Ichneumonoidea ind.			1					
Aculeata ind.					1			
Apocrita ind.	1							
Hymenoptera ind.	5				5			
Hymenoptera tot.	33	0.292	7	0.163	79	0.351	2	0.069
Empididae ind.					1			
Sciaridae ind.					7			
Tipulidae ind.					1			
Brachicera ind.					1			
Nematocera ind.							1	
Diptera tot.	0	0.000	0	0.000	10	0.044	1	0.034
Amara sp. (Carabidae)					1			
Carabidae ind.					2			

	FPA				SF			
	P. sicula		*P. muralis*		*P. sicula*		*P. muralis*	
	n	f	n	f	n	f	n	f
Silphidae ind.					2			
Psammobius sp. (Scarabaeidae)	1							
Aphodiinae ind. (Scarabaeidae)	2							
Scarabaeidae ind.					1			
Catomus rotundicollis (Tenebrionidae)					2			
Ammobius rufus (Tenebrionidae)					1			
Phaleria acuminata (Tenebrionidae)					1			
Tenebrionidae ind.					1			
Apioninae ind. (Curculionidae)					1			
Curculionidae ind.	3				2		1	
Bruchidae ind.							1	
Coleoptera ind.	7		2		5		0	
Coleoptera tot.	13	0.115	2	0.047	19	0.084	2	0.069
Insecta ind.	26		25		21		4	
Insecta tot.	97	0.858	37	0.860	196	0.871	15	0.517
Arthropoda ind.	2				4		1	
Arthropoda tot.	108	0.956	43	1.000	220	0.978	28	0.966
	113	1.000	43	1.000	225	1.000	29	1.000