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Helminth communities of two lizard populations (Lacertidae) from Canary Islands (Spain): Host diet-parasite relationships

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Abstract. A parasitological survey has been carried out to determine the relationships between host diet and parasite fauna. Diet, and infracommunities and component communities of two subspecies of lacertid lizards, *Gallotia galloti galloti* (Oudart, 1839) and *G. g. palmae* (Boettger et Müller, 1914) from Tenerife and La Palma islands (Canary Islands, Spain), have been analysed. High values of parasite infection parameters were found in both subspecies, which were only infected by nematodes of the family Pharyngodonidae. Plant matter was mainly consumed by both lizard subspecies and relevant amounts of mineral matter were also found in both hosts. Diet of these lacertid lizards was correlated with their parasite fauna formed by monoxenous nematodes parasitising herbivorous reptiles, as in tortoises and iguanid lizards. Abundance and richness of parasites increased with consumption of plant matter in *G. g. galloti*. Helminthological data support the idea of a tendency of both hosts towards herbivory, probably related to their own phylogeny linked to insularity.

Keywords: Lacertidae, *Gallotia galloti*, Parasites, Diet.

Introduction

At present, studies of helminth fauna of Canarian lacertid lizards have been scarce, partial and mainly from the point of view of taxonomy of parasites (Astasio-Arbiza et al., 1987, 1988, 1989; Roca et al., 1987; Solera-Puertas et al., 1988; Zapatero et al., 1999). Only recently, Roca et al. (1996, 1997), initiated ecological surveys on the helminth fauna of some of these Canarian reptiles. In *Gallotia galloti*, only a preliminary survey on helminth infracommunities of *G. galloti galloti* and *G. galloti palmae* has been carried out (Vela et al., 2000).

Some studies showed the relationships between diet of reptile hosts and their helminth faunas (Roca and Hornero, 1991; Roca, 1999). One of the most important aspects is the relationship between helminth fauna and consumption of plant matter by the host (carnivory – herbivory). The helminth faunas of carnivorous and herbivorous reptiles are different in two ways: (i) the infection by distinct species of nematodes of the family Pharyngodonidae; in this family, Petter and Quentin (1976) recognized two evolutionary lineages (with different genera in each one) parasitising carnivorous or herbivorous reptiles; (ii) the structure of helminth communities; they are more rich and diverse in herbivorous reptiles (Aho, 1990; Roca and Hornero, 1991).

The peculiarities in feeding habits of insular lacertid lizards have been reported by many authors (Pérez-Mellado and Corti, 1993; Brown and Pérez-Mellado, 1994), and reviewed by Van Damme (1999). Species or populations living on islands show a greater tendency towards herbivory than those on the mainland (Sadek, 1981; Van Damme, 1999) and, in some cases, lizards show a true specialisation towards this tendency (Carretero et al., 2001), related with a great infection by nematode parasites (Dearing, 1993). This tendency is more marked in old insular lineages such as *Gallotia* (Carretero, 2005).

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Thus in this paper, we analyse the helminth and diet parameters from *G. g. galloti* and *G. g. palmae*, specifically addressing the following issues: (i) characterisation of the patterns of helminth community richness and diversity; (ii) characterisation of the patterns of diet; (iii) relationships between helminths and diet, where we would expect that hosts harbour complex helminth fauna, including some typical parasites of herbivorous reptiles.

Materials and methods

Twenty-seven specimens of *G. g. galloti* (13 males, 12 females, and 2 juveniles), were collected by hand in the localities of San Cristobal de La Laguna and Valle de la Orotava (Tenerife Island) in February 1997. Twenty-seven specimens of *G. g. palmae* (8 males, 16 females, and 3 juveniles), were collected in Fuencaliente (La Palma Island) in January 1996. All lizards were caught in typical habitats of both volcanic islands, dominated by volcanic rocks and scattered bushes and called "malpaíses" (badlands). Lizards were transported alive to the laboratory. There, they were sacrificed humanely, dissected and their digestive tract, heart, lungs, and liver were removed and opened in Ringer's solution for microscopically examination. Helminthes were counted, washed in distilled water, fixed, mounted using standard techniques, and identified to species. Digestive contents were analysed under a binocular dissecting microscope. The minimum numbers criterion was used for prey counting (Escarré and Vericad, 1981). With some exceptions, the Order level was used as the operational taxonomic unit (OTU, Sneath and Sokal, 1973) for identification (see Tables).

The use of descriptive ecological terms follows Bush et al. (1997). Jover's method (Jover, 1989) was used in the statistical analysis of diet description and trophic diversity (see Carretero, 2005; Carretero and Llorente, 1991, 1993; Carretero et al., 2001). Four descriptors were calculated: the abundance (%P), the occurrence (%N), the probabilistic index (IP) and the resource use index (IU). The last one emphasizes the homogeneity as a criterion for evaluating the importance of the different OTUs (Jover, 1989). Overall parameters of both helminth infracommunities and diet for the two host subspecies were calculated as mean individual values and compared by mean of ANOVAs. Those parameters were: abundance (number of helminthes or prey items), richness (number of parasite species or OTU's), diversity and evenness. Brillouin's indices were used for calculating diversity and evenness according to Magurran (2004). For diet, populational diversity (Hp) was also estimated using the Jack-knife technique (Jover, 1989) and compared using T tests (Carretero and Llorente, 1991). A sequential Bonferroni correction (Rice, 1989) was applied when several tests were evaluated simultaneously.

Results

Helminth community

Only nematodes of the family Pharyngodonidae (Oxyuroidea) were found in the large intestine of both host subspecies. In total, seven nematode species were found, four of them being common to both hosts. The overall prevalence of infection of the *G. g. galloti* population was 77.8%, and was 92.6% for the *G. g. palmae* population. Prevalence, intensity of infection and abundance for each helminth species in each host, are shown in table 1. The overall diversity parameters of the nematode infracommunities of both hosts are indicated in table 3. The nematode component community of *G. g. palmae* is composed of 6 species, whereas only 5 species appeared in *G. g. galloti*. *G. g. palmae* shows more richness, diversity and uniform component community (*sensu* Bush et al., 1997) than *G. g. galloti* (table 4). Moreover, helminth community of adult females showed higher richness, diversity and evenness than adult males in both subspecies (table 4).

Diet

Table 2 shows the main diet descriptors for both subspecies of *Gallotia*. Both lizard populations were mainly herbivorous (89.68% of plant matter in *G. g. galloti* and 95.70% in *G. g. palmae*). *G. g. palmae* consumed significantly more plant matter than *G. g. galloti* but no sexual differences were found (2 way-ANOVA, factor subspecies $F_{1,45} = 5.39$, $p = 0.02$; factor sex $F_{1,45} = 3.13$, $p = 0.08$, n.s.; interaction $F_{1,45} = 6.14$, $p = 0.01$). Leaves were the most important plant item; sprouts and seeds were rarely consumed. Concerning the animal diet, the most important taxa were Coleoptera in *G. g. galloti* and Coleoptera, Miriapoda and Homoptera in *G. g. palmae*. Mineral matter was found in almost all the contents representing 7.88% of items in *G. g. galloti* and 3.16% in *G. g. palmae*.

The overall diversity parameters of diet are indicated for both hosts in table 3. Although in-

Table 1. Infection parameters of the helminthes parasitizing *Gallotia galloti galloti* and *G. g. palmae*. n = number of infected hosts. Exam = number of examined hosts. N = overall number of helminthes.

Host/helminth species	Prevalence		Intensity		Abundance	
	n/exam	%	Range	$\overline{X}$	N	$\overline{X}$
Gallotia galloti galloti						
Thelandros galloti	13/27	48.1	3-314	53.8	700	25.9
Alaeuris sp.	1/27	3.7	–	–	1	–
Parapharyngodon micipsae	4/27	14.8	1-7	4.25	17	0.6
Spauligodon atlanticus	9/27	33.3	2-98	32	288	10.7
Skrjabinodon medinae	2/27	7.4	3-12	7.5	15	0.6
Gallotia galloti palmae						
Thelandros galloti	20/27	74.1	1-119	27.3	545	20.2
Thelandros tinerfensis	15/27	55.6	2-196	29.4	441	16.3
Thelandros filiformis	1/27	3.7	–	–	47	–
Alaeuris sp.	10/27	37	1-103	25.2	252	9.3
Spauligodon atlanticus	16/27	59.3	1-157	37.4	599	22.2
Skrjabinodon medinae	2/27	7.4	1-7	4	8	0.3

Table 2. Diet descriptors of the two lizard subspecies. T: total number of prey items; %P: percentage of occurrence; %N: percentage of abundance; IP: probabilistic index; IU: resource use index (Jover, 1989).

OTUs	*Gallotia galloti galloti*					*Gallotia galloti palmae*				
	T	%P	%N	IP	IU	T	%P	%N	IP	IU
seeds	18	7.4	0.9	0.07	0.11	24	18.5	0.9	0.05	0.37
Araneae	6	22.2	0.3	0.3	0.2	3	11.1	0.1	0	0.04
Lepidoptera	1	3.7	0.1	0.08	0	3	11.1	0.1	0	0.04
Coleoptera	34	55.6	1.8	2.95	1.5	8	29.6	0.3	0	0.20
Diptera	1	3.7	0.1	0.06	0	–	–	–	–	–
Acarina	4	11.1	0.2	0.03	0.07	2	7.4	0.1	0.01	0.02
Miriapoda	9	29.6	0.4	0.2	0.33	15	11.1	0.5	1.28	0.18
Homoptera	1	3.7	0.1	0.08	0	14	11.1	0.5	0.04	0.18
Heteroptera	1	3.7	0.1	0.02	0	–	–	–	–	–
Formicidae	7	22.2	0.4	0.03	0.2	7	7.4	0.2	0.01	0.04
plant matter	1679	96.3	87.3	91.58	89.68	2542	92.6	91.8	96.05	95.70
unidentified	–	–	–	–	–	7	14.8	0.2	0	0.07
mineral matter	157	62.9	8.1	4.52	7.88	112	48.1	4.0	2.33	3.16

Table 3. Overall diversity parameters of parasite fauna and diet of both hosts. [1] One of the lizards lacked prey in the digestive tract then preventing the calculation of diversity and evenness.

Parameter	*Gallotia galloti galloti*		*Gallotia galloti palmae*	
	n	mean ± SE (range)	n	mean ± SE (range)
Parasites				
abundance	27	37.81 ± 12.86 (0-314)	27	70.07 ± 15.72 (0-373)
richness	27	1.07 ± 0.15 (0-3)	27	2.37 ± 0.21 (0-4)
diversity	27	0.16 ± 0.06 (0-0.94)	27	0.75 ± 0.11 (0-1.86)
evenness	27	0.11 ± 0.04 (0-0.65)	27	0.52 ± 0.08 (0-1.29)
Diet				
abundance	27	65.33 ± 8.82 (6-127)	27	98.37 ± 7.54 (0-127)
richness	27	2.59 ± 0.23 (1-5)	27	2.22 ± 0.23 (0-5)
Indiv. diversity	27	0.36 ± 0.07 (0-1.25)	26[1]	0.17 ± 0.04 (0-0.75)
pop. diversity	–	0.38 ± 0.09 (jack-knife)	–	0.29 ± 0.06 (jack-knife)
evenness	27	0.21 ± 0.04 (0-0.62)	26[1]	0.12 ± 0.02 (0-0.47)

Table 4. ANOVA (and T) comparisons for the overall parameters of parasite fauna and diet. Results in bold are significant.

	Parameter	host subspecies		host sex		interaction	
		$F_{\text{d.f.}}$	p	$F_{\text{d.f.}}$	p	$F_{\text{d.f.}}$	p
Parasites	Abundance	$F_{1,45} = 2.47$	0.12	$F_{1,45} = 0.01$	0.92	$F_{1,45} = 0.58$	0.45
	Richness	$F_{1,45} = 34.07$	$5 * 10^{-7}$	$F_{1,45} = 8.88$	0.004	$F_{1,45} = 0.70$	0.40
	Diversity	$F_{1,45} = 21.17$	$3 * 10^{-5}$	$F_{1,45} = 5.33$	0.03	$F_{1,45} = 0.26$	0.61
	Evenness	$F_{1,45} = 21.16$	$3 * 10^{-5}$	$F_{1,45} = 5.33$	0.03	$F_{1,45} = 0.26$	0.61
Diet	Abundance	$F_{1,45} = 5.51$	0.02	$F_{1,45} = 3.49$	0.07	$F_{1,45} = 6.78$	0.01
	Richness	$F_{1,45} = 0.62$	0.44	$F_{1,45} = 0.30$	0.59	$F_{1,45} = 0.80$	0.37
	Indiv. diversity	$F_{1,44} = 2.48$	0.12	$F_{1,44} = 1.51$	0.23	$F_{1,44} = 0.72$	0.40
	Pop. diversity	$T_{44} = 0.07$	0.47				
	Evenness	$F_{1,44} = 1.60$	0.21	$F_{1,44} = 1.59$	0.21	$F_{1,44} = 1.75$	0.19

dividual diversity was lower than populational, differences remained scarce. Except for the low prey abundance in male *G. g. galloti* when compared to other groups no other significant differences, neither between subspecies nor between sexes, appeared (table 4).

Host diet-parasite relationships

Helminth fauna of *Gallotia galloti* was associated with the amount of plant matter eaten by lizards at the individual level. A correlation between several general parameters of helminth fauna (abundance and richness) and diet was found in *G. g. galloti* (table 5), but not in *G. g. palmae*. Furthermore, abundance and richness of parasites increased with consumption of plant matter in *G. g. galloti* (table 6). When considering each parasite species isolate, only *Telandros galloti* was found to be positively correlated with the amount of plant matter in both subspecies whereas *Thelandros filiformis* was negatively correlated in *G. g. palmae* (table 6).

Qualitatively, only monoxenous nematodes of family Pharyngodonidae were found parasitizing both subspecies (see table 1). Neither Cestodes nor Trematodes were found.

Discussion

Helminth community diversity

The diversities of helminth infracommunities in both host populations are different. Diversity of helminth infracommunity of *G. g. galloti* is similar to other helminth diversities of insular reptiles of the genera *Tarentola* and *Podarcis* (Roca, 1999). Nevertheless, value of Brillouin's index of helminth infracommunity of *G. g. palmae*, is higher because abundance and species richness (table 3).

Although 6 and 5 nematode species were recorded respectively from *G. g. palmae* and *G. g. galloti* (component communities), the average number per lizard never exceeded 2.37 and 1.07, respectively, and the maximum number of species found in any individual lizard was 4 and 3, respectively (table 3). So, no single infracommunity included all species locally available. This suggests, for both subspecies of *G. galloti*, saturation of infracommunities with the parasite species at levels below the component community richness (Poulin, 1998), a typical pattern found in many reptiles (Roca, 1999; Roca and Hornero, 1994).

Both hosts harbour relatively homogeneous component communities. This suggests frequent exchanges of parasites between both host populations of the same species (Poulin, 1998). As they are isolated from one another [these two subspecies are geographically and temporally separated; thus, the islands of Tenerife and La Palma are 12-16 My and 2 My old respectively (Barahona et al., 2000); divergence time between both subspecies has been calculated as 0.3 My (Thorpe et al., 1993)], we can explain that homogeneity in two non exclusive

Table 5. Correlation matrix between the overall parameters of diet and parasite fauna. *Significant when considered isolately, **significant after applying sequential Bonferroni adjustment.

		Abund. diet	Richness diet	Diversity diet	Evenness diet
Gallotia galloti galloti $n = 27$	abundance parasites	0.43 $p = 0.02$*	−0.11 $p = 0.59$	−0.15 $p = 0.43$	−0.22 $p = 0.27$
	richness parasites	0.53 $p = 0.004$**	0.12 $p = 0.56$	−0.23 $p = 0.24$	−0.23 $p = 0.24$
	diversity parasites	0.28 $p = 0.15$	0.06 $p = 0.77$	−0.13 $p = 0.52$	−0.13 $p = 0.50$
	evenness parasites	0.28 $p = 0.15$	0.06 $p = 0.77$	−0.13 $p = 0.52$	−0.13 $p = 0.50$
Gallotia galloti palmae $n = 26$	abundance parasites	0.17 $p = 0.40$	0.16 $p = 0.44$	0.18 $p = 0.38$	0.16 $p = 0.42$
	richness parasites	−0.12 $p = 0.56$	0.05 $p = 0.81$	0.14 $p = 0.50$	0.20 $p = 0.32$
	diversity parasites	−0.07 $p = 0.73$	−0.07 $p = 0.73$	0.11 $p = 0.60$	0.21 $p = 0.31$
	evenness parasites	−0.07 $p = 0.73$	−0.07 $p = 0.73$	0.11 $p = 0.60$	0.21 $p = 0.31$
Total $n = 53$	abundance parasites	0.36 $p = 0.008$**	0.005 $p = 0.97$	−0.09 $p = 0.50$	−0.11 $p = 0.44$
	richness parasites	0.38 $p = 0.005$**	−0.004 $p = 0.97$	−0.22 $p = 0.11$	−0.17 $p = 0.22$
	diversity parasites	0.28 $p = 0.04$*	−0.08 $p = 0.56$	−0.17 $p = 0.22$	−0.11 $p = 0.43$
	evenness parasites	0.28 $p = 0.04$*	−0.08 $p = 0.56$	−0.17 $p = 0.22$	−0.11 $p = 0.43$

Table 6. Correlations between plant matter consumption and parasite fauna. *Significant when considered in isolate, **significant after applying sequential Bonferroni adjustment.

	(plant matter)		
	G. g. galloti $n = 27$	*G. g. palmae* $n = 27$	total $n = 54$
Thelandros galloti	0.40 $p = 0.04$*	0.41 $p = 0.04$∗	0.33 $p = 0.01$**
Spauligodon atlanticus	0.12 $p = 0.56$	−0.01 $p = 0.94$	0.10 $p = 0.46$
Parapharyngodon micipsae	−0.12 $p = 0.56$	–	−0.17 $p = 0.21$
Alaeuris sp.	0.14 $p = 0.48$	0.13 $p = 0.51$	0.17 $p = 0.21$
Skrjabinodon medinae	0.16 $p = 0.42$	0.13 $p = 0.52$	0.11$p = 0.43$
Thelandros tinerfensis	–	0.12 $p = 0.55$	0.17 $p = 0.21$
Thelandros filiformis	–	−0.47 $p = 0.01$**	−0.23 $p = 0.09$
abund. parasites	0.42 $p = 0.03$*	0.18 $p = 0.37$	0.35 $p = 0.01$**
richness parasites	0.51 $p = 0.007$**	−0.25 $p = 0.20$	0.27 $p = 0.04$*
diversity parasites	0.27 $p = 0.17$	−0.21 $p = 0.28$	0.18 $p = 0.19$
evenness parasites	0.27 $p = 0.17$	−0.21 $p = 0.28$	0.18 $p = 0.19$

ways: (i) the easy of dispersion of eggs of nematodes between islands; (ii) evolutionary short time passed since separation of both populations is still insufficient for divergence of component communities. In any case, this homogeneity confirms the hypothesis of Thorpe et al. (1994) about the processes of colonisation of western Canary Islands by lizards.

Diet

Although some animal items are present, both lizard subspecies but especially *G. g. palmae* can be considered mainly herbivorous. This condition is extremely rare in lizards (King, 1996) but common in the genus *Gallotia* (Valido and Nogales, 1994; Molina-Borja, 1986; Pérez-Mellado et al., 1999). Valido and Nogales (2003) consider *G. galloti* to be omnivorous rather than herbivorous, and concluded that body size is the major determinant explaining the level of herbivory in these lizards. In any case, herbivory (or plant matter consumption) applies especially to adult lizards of both sexes; juvenile lizards consume more animal matter as a result of physiological and anatomical constraints (Pough, 1973; Carretero, 1997). However, we have detected some differences in the diet between the two lizard subspecies. Thus, *G. g. galloti* eat lower quantities of Diptera and Heteroptera and higher quantities of Coleoptera than *G. g. palmae*. On the other hand, Homoptera, one aggregated prey, are more consumed by *G. g. palmae* than *G. g. galloti*.

Host diet – parasite relationships

Nematodes of the family Pharyngodonidae are indicative of the feeding habits of the reptile hosts (Petter and Quentin, 1976). The genera *Pharyngodon*, *Spauligodon*, *Skrjabinodon*, *Parapharyngodon*, and *Parathelandros* belong to an evolutionary lineage parasitising carnivore saurians, whereas *Tachygonetria*, *Mehdiella*, *Alaeuris*, *Thaparia*, *Ortleppnema*, *Ozolaimus*, *Travassozolaimus*, and *Mamillomacracis* parasitize herbivore iguanids and tortoises. Both hosts, *G. g. galloti* and *G. g. palmae* combine in their helminth communities genera of both lineages. Thus, *Spauligodon*, *Skrjabinodon* (and *Parapharyngodon* in the case of *G. g. galloti*) are joined with *Alaeuris*.

The species of *Thelandros* parasitizing both hosts do not provide useful information because this genus parasitizes both carnivorous and herbivorous reptiles (Petter, 1966), although Roca (1999) never found it neither in the more typically herbivorous reptile *Testudo graeca*, nor in other insectivorous Palaearctic reptiles of the families Lacertidae and Gekkonidae. Our results suggest that species of the genus *Thelandros* may be typical of herbivorous lacertid lizards.

This structure of helminth communities suggests gradual tendency from carnivory towards herbivory in these lizards, considering the origin of the genus *Gallotia* from a carnivorous ancestral, similar to the present genus *Psammodromus*, the sister group of *Gallotia* (Harris et al., 1998), constituted by very generalised lizards living in Iberian Peninsula and NW Africa. This tendency is reflected in an important consumption of vegetal matter by both subspecies higher than in any other lacertid except those belonging to the genus *Gallotia* (see previous references). In addition, the presence of mineral matter in the digestive tract of these lacertid lizards, emphasises the herbivore character of their diet; mineral matter has been found in herbivorous tortoises and this has been interpreted as an aid for mechanical digestion (Marlow and Tollestrup, 1982; Roca et al., 1988).

In reptile hosts, other relationships between feeding habits and parasites have been pointed out by Roca and Hornero (1991). An herbivorous diet involves some peculiar features of helminth component community such as: (i) no helminth species with indirect life cycles; (ii) scarce taxonomic variation at the family level; (iii) high values of intensity of infection and of abundance and richness of helminth species. Both populations of *G. galloti* are parasitized only by monoxenous nematodes of the family Pharyngodonidae. Moreover, values of mean infection intensity of most helminth species are higher than values showed by the same or similar Pharyngodonidae species parasitising insular insectivorous lizards of the genus *Podarcis* (Roca and Hornero, 1994). Values of abundance and species richness are also higher in *G. galloti* than in other insectivorous reptiles (Roca, 1999).

In conclusion, both subspecies *G. g. galloti* and *G. g. palmae* from Tenerife and La Palma islands respectively, show a strong tendency towards herbivory probably deriving from a long evolutionary history of the genus *Gallotia* under insular conditions (Carranza, 2002; Carretero, 2005). Furthermore, this tendency is also found at the individual level, which suggest dynamic relationships between diet and helminthes (i.e. the increase of plant matter consumed, provides a suitable environment for the development of a more rich and abundant helminth fauna). This last aspect deserves further investigation extending the analysis to the rest of the year and to other *Gallotia* species.

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