

Relationships between helminth communities and diet in Canarian lizards: the evidence from *Gallotia atlantica* (Squamata: Lacertidae)

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Diet and helminth fauna were analysed in the lizard *Gallotia atlantica* (Squamata: Lacertidae), the smallest species of this genus endemic to Lanzarote and Fuerteventura (Canary Islands), in an attempt to confirm previous claims of relationships between these ecological traits in this genus. A total of 70 lizards belonging to the subspecies *atlantica* (central southern Lanzarote), *laurae* (northern Lanzarote) and *mahoratae* (Fuerteventura) were examined. Compared with other *Gallotia*, the helminth fauna was impoverished, particularly in Fuerteventura, where the absence of larval cestodes suggests low predation pressure. Diet was omnivorous, the plant fraction (73.03–84.26%) included seeds and fruits while the animal fraction was quite diverse, at least in Lanzarote. Contrary to other *Gallotia*, the intestinal Pharyngodonidae nematodes were all typical of carnivorous reptiles. An individual association between the complexities of helminth communities and diet reinforces previous findings in other *Gallotia* species suggesting functional relationships between parasites and prey items inside the digestive tract.

Keywords: Canary Islands; helminth community; diet composition; diet-parasites relationship; Lacertidae

Introduction

Increasing evidence is indicating that initial ideas on the frequency of herbivory in reptiles and the interlaying evolutionary processes promoting its origin were incomplete if not completely biased (King 1996; Cooper and Vitt 2002; Vitt 2004); especially with regard to the consumption of plant matter by lizards. Although herbivory was once considered to be restricted to large, highly specialized species (Pough 1973), records of the number of small lizards eating plant parts but lacking anatomical specializations for herbivory increase day by day (Cooper and Vitt 2002). Documenting the trophic patterns of species and the effects that these have on other aspects of the lizards' biology within a proper comparative framework is now needed to establish new hypotheses for the origin of herbivory in saurian taxa. In this regard, the family Lacertidae in general and the genus *Gallotia* in particular are of special interest (Roca 1999; Carretero 2004).

The genus *Gallotia* constitutes a clade of seven extant (plus two extinct) species of insular lizards endemic to the Canary Islands (Mateo et al. 2007). From a

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phylogenetic point of view, it represents an old, separate radiation evolving independently from other members of the family Lacertidae except from the continental genus *Psammodromus*, which is not closely related (Arnold et al. 2007). *Gallotia* lizards display many original anatomical and ecological features not found in other lacertids, including extremely large body sizes and the consumption of an abundant proportion of plant matter (Mateo et al. 2007).

Moreover, *Gallotia* lizards harbour in their intestines the richest helminth fauna reported for lacertids (Roca 1999). Previous studies performed on several species from central and western islands support relationships between their diet and helminth parasites (Martin et al. 2005; Roca et al. 2005; Carretero et al. 2006). However, the comparative data set is still incomplete. Namely, no equivalent studies are available for *Gallotia atlantica* (Peters and Doria 1882), for which only general diet descriptions (Valido and Nogales 2003) and isolated reports of parasites (Astasio-Arbiza et al. 1987; Roca 2003; Abreu-Acosta et al. 2006) are available. This lizard species inhabits the eastern islands of the archipelago, Lanzarote and Fuerteventura. From a phylogenetic point of view, it is not directly related to other *Gallotia* spp., neither is it the sister taxon of all remaining species as its distribution on the oldest islands of the archipelago would suggest (Cox et al. 2010). Of the three currently accepted subspecies of *G. atlantica* inhabiting the main islands, there is strong genetic support for the distinction between the populations from Fuerteventura (*G. a. mahoratae*) and those from Lanzarote (Maca-Meyer et al. 2003; Mateo et al. 2007; Cox et al. 2010). However, the status of the subspecies *G. a. laurae* from northern Lanzarote as compared to the nominal subspecies occupying the remaining parts of the island has been a matter of debate (López-Jurado 1991; Mateo et al. 2007; Bloor et al. 2008) because of the lower genetic divergence (González et al. 1996; Maca-Meyer et al. 2003). Furthermore, palaeogeological reconstructions suggest that Lanzarote and Fuerteventura were closer together, if not connected, during glaciations (Villalba 1998), allowing interchanges between lizard (and therefore parasite) populations.

Finally, from an ecological point of view, because of the old age of both islands, there has been erosion of the main relief, and both islands now differ from the rest of the archipelago in being unable to retain the humidity carried by the dominant trade winds (Juan et al. 2000) and, hence, have arid conditions, which are especially harsh in Fuerteventura.

This original scenario in terms of evolution, biogeography and ecology poses special constraints for the development of herbivory and the formation of parasite communities. From the point of view of feeding habits, lacertids living on islands show a trend towards herbivory compared with their relatives on the mainland (Van Damme 1999). Where evolution has occurred for long periods under insular conditions, as in the case of *Gallotia* lizards, true specializations involving anatomy and behaviour have arisen (Carretero et al. 2001; Olesen and Valido 2003; Carretero 2004; Herrel et al. 2004). With respect to intestinal parasites, it has been suggested (Roca 1999) that the monoxenous life cycle typical of Pharyngodonidae nematodes favours the infection of herbivorous reptile hosts because they have more opportunities to accidentally eat eggs deposited in plants through faecal pellets. Also, the increase of plant matter consumed provides a suitable environment for the development of a more rich and abundant helminth fauna (Petter and Quentin 1976; Roca 1999; Roca et al. 2005; Carretero et al. 2006). In fact, previous studies of host

diet–parasite relationships (Martin et al. 2005; Roca et al. 2005; Carretero et al. 2006) have demonstrated that some *Gallotia* species not only harbour rich helminth infra-communities but also that the complexities of parasite communities and diet (and especially the plant fraction) are associated.

Hence, the objective of this study was to investigate the relationships between helminth and diet parameters within *G. atlantica* across the species range. More specifically, this study aimed: (1) to determine the patterns of helminth community richness and diversity; (2) to characterize the patterns of dominance and diversity in the diet; (3) to evaluate the degree of variation of parasite infestation and diet between subspecies, sexes and size classes; and, finally, (4) to determine whether relationships between helminths and diet exist. Regarding this last point, our hypothesis is that, as *G. atlantica* belongs to an ancient insular lineage but attains the smallest size within the genus, it should harbour simpler herbivorous helminth faunas than other *Gallotia* spp. but still richer than those of continental lacertids. Such parasite diversity would arise from present or past functional relationships with the consumption of plant matter.

Material and methods

Specimens of the subspecies *G. a. atlantica*, *G. a. lauræ* and *G. a. mahoratae* collected in pitfall traps and deposited at the collections of the Department of Animal Biology (Vertebrates) of the University of Barcelona, Spain (DZV) and CIBIO, University of Porto (DB) were analysed. Specimens had been previously collected from Lanzarote (*G. a. atlantica*, Nazaret and Yaiza DZV-LZ54-73 and DBZ-LZ11-134; *G. a. lauræ*, Orzola DZV-LZ-75-88) and Fuerteventura (*G. a. mahoratae* Tefia, La Oliva, Lazares DB1242-1398) from representative localities (Figure 1). Both islands belong to the Canarian Archipelago, located off the northwest coast of Africa, at 27°37'–29°24' N,

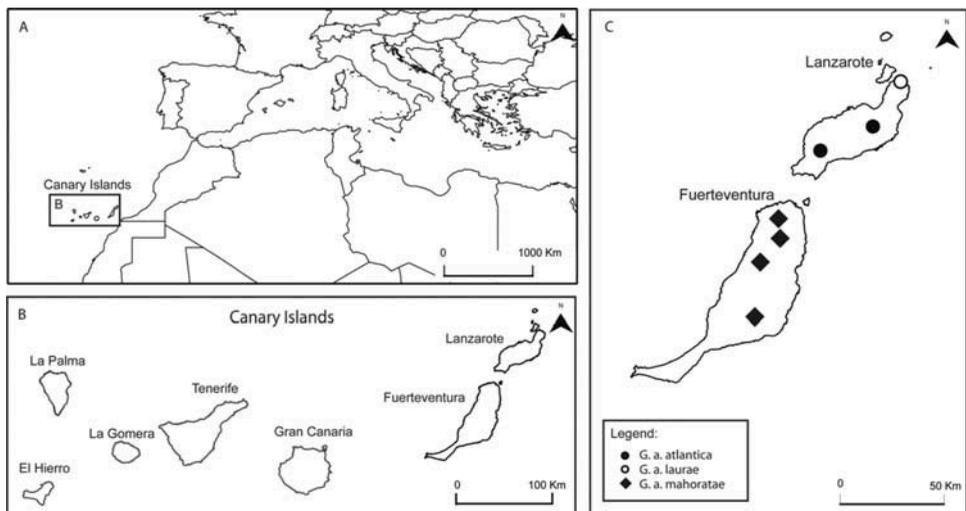


Figure 1. Location of the islands and sampling sites where the different subspecies were collected.

13°37'–8°10' W. These are volcanic islands, with an eastern peripheral position in the archipelago (Figure 1). Lanzarote has a surface of 846 km² and attains a maximum elevation of 670 m above sea level, while Fuerteventura covers 1665 km² and attains 807 m above sea level (Fernández-Palacios and Martín 2001). The typical habitat occupied by the mentioned subspecies of *G. atlantica* consists of xerophytic areas dominated by volcanic rocks and scattered bushes. *Gallotia a. atlantica* is distributed throughout most of Lanzarote whereas *G. a. laurae* is restricted to a small area in the north of this island. *Gallotia a. mahoratae* inhabits the whole Fuerteventura island (López-Jurado 1991; García-Márquez and Mateo 2002).

For a total of 70 lizards, 30 *G. a. atlantica* (16 adult males, six adult females and eight immatures), 13 *G. a. laurae* (four adult males, five adult females, four immatures) and 27 *G. a. mahoratae* (18 adult males, six adult females and three immatures) a parallel analysis of diet and intestinal parasites was conducted. The snout–vent length of the vouchers was measured with a digital calliper to the nearest 0.01 mm. Lizards were divided into three sex/size classes, adult male, adult female and immature on the basis of their body lengths (Carretero and Llorente 1993), sexual secondary characters (Molina-Borja 2003) and gonad inspection (Molina-Borja and Rodríguez-Domínguez 2004). In our sample of adult lizards, both size differences between subspecies and sexual size dimorphism, invariant across them, were detected (two-way analyses of variance subspecies $F_{2,49} = 15.45$, $p = 0.000006$; sex $F_{1,49} = 5.99$, $p = 0.02$; subspecies * sex $F_{2,49} = 0.27$, $p = 0.76$). Namely, males were bigger than females, while size (mean \pm SE) gradually decreased from *G. a. atlantica* (males 80.66 \pm 2.46 mm; females 73.00 \pm 2.11 mm) to *G. a. laurae* (males 73.50 \pm 5.33 mm; females 65.00 \pm 1.52 mm) and to *G. a. mahoratae* (males 63.95 \pm 1.97 mm; females 60.29 \pm 1.92 mm).

Lizards were dissected and their digestive tracts were removed and opened in Ringer's solution for examination. Digestive contents were analysed under a binocular dissecting microscope. For the diet analysis, the minimum-number criterion was used for prey counting of animal items and seeds (Carretero 2004). Other plant matter was counted as fragments because herbivorous lizards pierce leaf and stem pieces, in the same way as they do with animal prey, rather than chewing them (Herrel et al. 1998). This allowed animal and plant matter to be analysed together. With some exceptions, the Order level was used as the operational taxonomic unit (Sneath and Sokal 1973) for identification (see Table 1). Although residence time in the gut may differ between operational taxonomic units according to their digestibility (Mackie 2002), it is assumed that such bias would be minimal when comparing, as here, the same digestive compartment between subspecies and classes (Carretero and Llorente 2001). In parallel, helminths inside the digestive tract were counted, washed in distilled water, fixed, mounted using standard techniques (Roca 1985), and identified to species. Despite its invasiveness, this method still provides a more accurate representation of helminth communities than examination of faeces (Jorge et al. 2013) and is applicable to common lizard species that do not have threatened conservation status. The parasite vouchers were deposited in the parasitological collection of the Department of Zoology of University of Valencia, Spain, with the species name accompanied by the host code.

The following descriptors were calculated for both diet and helminth infracommunity for the entire sample of each lizard subspecies as well as separated by classes:

Table 1. Descriptors of parasite fauna and diet of *Gallotia atlantica* considering the three subspecies accepted.

Operational taxonomic units	<i>G. a. atlantica</i>				<i>G. a. laurae</i>				<i>G. a. mahoratae</i>			
	N	%P	%N	IU	N	%P	%N	IU	N	%P	%N	IU
Parasites												
<i>Pseudoparadistomum yaizaensis</i>	93	10.00	10.13	5.51	0	—	—	—	0	—	—	—
<i>Parapharyngodon micipsae</i>	3	3.33	0.33	0.00	4	15.38	2.41	0.99	0	—	—	—
<i>Parapharyngodon echinatus</i>	128	36.67	13.94	13.22	108	38.46	65.06	86.69	0	—	—	—
<i>Parapharyngodon bulbosus</i>	0	—	—	—	0	—	—	—	124	59.26	74.70	80.63
<i>Spauligodon atlanticus</i>	575	46.67	62.64	77.05	0	—	—	—	40	25.93	24.10	19.37
<i>Skrjabinelazia</i> sp.	0	—	—	—	0	—	—	—	2	3.70	1.21	0.00
<i>Mesocestoides</i> sp.	0	—	—	—	3	7.69	1.81	0.00	0	—	—	—
<i>Dipylidium</i> sp.	100	6.67	10.89	4.22	11	15.38	6.63	2.93	0	—	—	—
<i>Diplopylidium acanthotetra</i>	19	3.33	2.07	0.00	40	23.08	24.10	9.38	0	—	—	—
Diet												
Seeds	20	23.33	2.67	2.36	22	23.08	13.75	17.85	37	44.44	2.97	2.75
Plant matter	580	46.67	77.54	82.24	108	53.85	67.50	43.39	952	51.85	76.34	73.28
Coleoptera	13	33.33	1.74	2.21	4	23.08	2.50	4.16	82	85.19	6.58	9.04
Orthoptera	0	—	—	—	7	38.46	4.38	14.61	4	14.81	0.32	0.23
Hymenoptera	0	—	—	—	0	—	—	—	35	70.37	2.81	3.84
Formicidae	102	40.00	13.64	10.24	4	23.08	2.50	2.58	38	29.63	3.05	1.84
Diptera	0	—	—	—	3	23.08	1.88	1.38	7	18.52	0.56	0.43
Lepidoptera	1	3.33	0.13	0.00	0	—	—	—	18	55.56	1.44	1.91
Heteroptera	15	16.67	2.01	1.28	6	23.08	3.75	1.43	18	51.85	1.44	1.79
Larvae	2	6.67	0.27	0.11	0	0.00	0.00	0.00	8	29.63	0.64	0.68
Pupae	1	3.33	0.13	0.00	0	0.00	0.00	0.00	11	33.33	0.88	0.88
Araneida	1	3.33	0.13	0.00	3	15.38	1.88	2.98	27	59.26	2.17	2.69
Arthropoda not identified	9	26.67	1.20	1.46	0	—	—	—	—	—	—	—
Gastropoda	2	6.67	0.27	0.11	1	7.69	0.63	0.01	10	22.22	0.80	0.66
Vertebrata	2	3.33	0.27	0.00	2	15.38	1.25	11.62	0	0.00	0.00	0.00

Notes: N: total number of prey items (intensity); %P: percentage of occurrence (prevalence); %N: percentage of abundance; IU: resource use index (Jover 1989; Carretero 2004).

prevalence or occurrence (%*P*, percentage of lizards with prey/parasite items), relative abundance (%*N*, percentage of each prey or parasite item), and resource use index (Jover 1989). The latter index emphasizes the homogeneity as a criterion for evaluating the importance of the different operational taxonomic units (Carretero et al. 2001; Carretero 2004). The use of descriptive ecoparasitological terms follows Bush et al. (1997). Brillouin's indices were applied for calculating diversity and evenness of diet and parasite communities according to Magurran (2004). Population diversity (*H*_p) was also estimated by a Jack-knife procedure (Jover 1989; Carretero 2004) and compared between sexes by *t*-tests due to the non-additive nature of diversity (Carretero 2004; Martin et al. 2005; Roca et al. 2005; Carretero et al. 2006). All the parameters were calculated as mean individual values and compared through an analysis of variance. Additionally, as relationships between lizards' body size and both diet and parasite communities have been reported for other *Gallotia* species (Martin et al. 2005; Roca et al. 2005; Carretero et al. 2006), snout-vent length was also used as a covariate in an analysis of covariance. In all cases, variables were previously log-transformed to ensure normality and homoscedasticity (assessed by Lilliefors' and Levene's tests, respectively). When evaluating simultaneously sets of pairwise correlations or mean comparisons, we applied a false discovery rate procedure (Benjamini and Hochberg 1995) to correct for multiple tests without inflating Type II error (Moran 2003; Nakagawa 2004).

Results

Helminth communities

In total, nine helminth species were found in the three host subspecies searched (Table 1). The global infection prevalences were 80.8% for *G. a. atlantica*, 72.2% for *G. a. laurae* and 81.5% for *G. a. mahoratae*. The cestodes *Diplopylidium acanthotetra*, *Dipylidium* sp. and *Mesocostoides* sp. were found as larval forms in the body cavity of the hosts. The digenea *Pseudoparadistomum yaizaensis* and the nematode *Skrjabinelazia hoffmanni* were found in the small intestine, and the nematodes *Spauligodon atlanticus* (*sensu stricto*, see Jorge et al. 2011, 2013), *Parapharyngodon echinatus*, *Parapharyngodon micipsae* and *Parapharyngodon bulbosus*, in the rectum. Infection values of each parasite species greatly varied with the host subspecies but, only *Pseudoparadistomum yaizaensis* was host-specific, namely of *G. a. atlantica*. It is also noteworthy that our samples of *G. a. laurae* and *G. a. mahoratae* did not share any parasite species but both shared some with *G. a. atlantica*.

The diversity parameters of the helminth infracommunities of the three host subspecies are indicated in Table 2. Except for individual diversity, which was weakly correlated ($r = 0.24$, $T_{69} = 2.08$, $p = 0.04$), the remaining diversity parameters were uncorrelated with lizard size. Individual diversity attained much lower (three to four times) values than population diversity for the three subspecies. The comparisons between subspecies and classes (Table 3, Figure 2) indicated no intraspecific variation for the intensity but detected significant differences across subspecies for richness (interacting with class), individual diversity and evenness. In most cases, post-hoc tests lacked sufficient statistical power to discriminate the significant pair differences except for the evenness, which was lower in *G. a. mahoratae* than in *G. a. atlantica* (Scheffé tests $p < 0.05$) mainly due to the low values of the immature lizards in both

Table 2. Diversity parameters of parasite fauna and diet in *Gallotia atlantica*.

Parameter	<i>G. a. Atlantica</i>		<i>G. a. laurae</i>		<i>G. a. mahoratae</i>	
	N	Mean ± SE (range)	N	Mean ± SE (range)	N	Mean ± SE (range)
Parasites						
Abundance	13	30.50 ± 7.32 (0–156)	13	12.77 ± 4.53 (0–42)	20	6.15 ± 1.33 (0–27)
Richness	13	1.07 ± 0.15 (0–3)	13	1.00 ± 0.36 (0–4)	20	0.89 ± 0.10 (0–2)
Individual diversity	13	0.07 ± 0.02 (0–0.39)	13	0.06 ± 0.03 (0–0.37)	20	0.01 ± 0.01 (0–0.15)
Population diversity	–	2.19 ± 0.08 (Jack-knife)	–	2.24 ± 0.18 (Jack-knife)	–	2.12 ± 0.11 (Jack-knife)
Evenness	13	0.21 ± 0.06 (0–0.95)	13	0.11 ± 0.06 (0–0.61)	20	0.03 ± 0.02 (0–0.48)
Diet						
Abundance	30	24.93 ± 8.07 (0–182)	13	12.31 ± 4.98 (1–62)	27	46.19 ± 12.56 (4–240)
Richness	30	2.13 ± 0.22 (0–4)	13	2.46 ± 0.33 (1–5)	27	5.67 ± 0.34 (2–9)
Individual diversity	30	0.19 ± 0.02 (0–0.36)	13	0.16 ± 0.04 (0–0.46)	27	0.37 ± 0.03 (0.07–0.67)
Population diversity	–	1.20 ± 0.27 (Jack-knife)	–	1.72 ± 0.59 (Jack-knife)	–	1.48 ± 0.29 (Jack-knife)
Evenness	30	0.30 ± 0.05 (0–0.83)	13	0.35 ± 0.07 (0–0.68)	27	0.52 ± 0.04 (0.08–0.73)

Table 3. Analyses of variance and covariance (AN(C)OVA) comparisons for the abundance, richness and diversity of parasites and diet in *Gallioia atlantica*, considering subspecies and class (adult males, adult females and immatures). For each parameter, the first line indicates the uncorrected analysis and the second the size-corrected analysis.

Parameter	ANOVA/ANCOVA(snout-vent length)									
	ssp.		class		ssp.*class					
	F	df	p	F	df	p	F	df	p	p
Parasites										
Abundance	2.73	2,61	0.07	2.51	2,61	0.09	1.27	4,61	0.29	0.29
	0.74	2,64	0.48	1.80	2,64	0.17				
Richness	0.86	2,61	0.43	1.57	2,61	0.22	2.82	4,61	0.03	0.03
	0.43	2,64	0.65	1.02	2,64	0.36				
Individual diversity	3.17	2,61	0.05	0.77	2,61	0.47	0.79	4,61	0.53	0.53
	0.90	2,64	0.41	0.40	2,64	0.53				
Evenness	4.35	2,61	0.02	0.84	2,61	0.44	0.95	4,61	0.44	0.44
	3.83	2,64	0.03	1.42	2,64	0.25				
Diet										
Abundance	1.91	2,61	0.15	3.62	2,61	0.03	0.47	4,61	0.46	0.46
	6.14	2,64	0.04	0.0005	2,64	0.99				
Richness	29.49	2,61	<10 ⁻⁶	1.20	2,61	0.31	0.52	4,61	0.72	0.72
	21.41	2,64	<10 ⁻⁶	0.10	2,64	0.91				
Individual diversity	133.61	2,61	<10 ⁻⁶	0.11	2,61	0.90	0.51	4,61	0.68	0.68
	10.29	2,64	0.0001	0.20	2,64	0.82				
Evenness	4.99	2,61	0.01	0.43	2,61	0.66	0.75	4,61	0.56	0.56
	0.37	2,64	0.04	0.95	2,64	0.39				

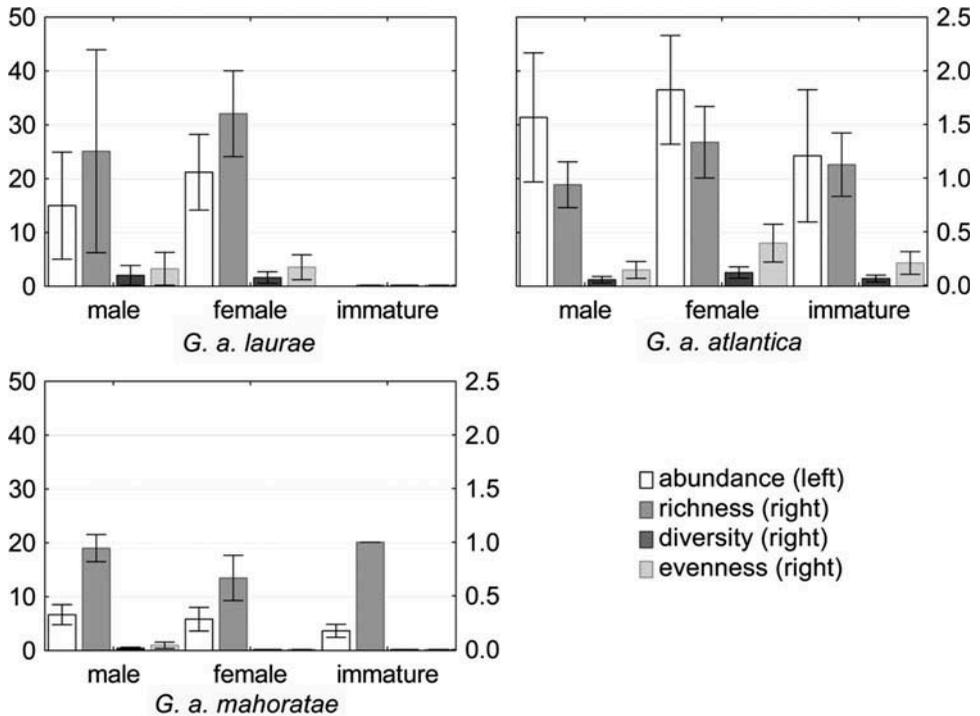


Figure 2. Variation of the parameters of parasite diversity in *Gallotia atlantica* considering the subspecies and class of the lizard host.

subspecies. These results persisted when the effect of lizard size was statistically removed (Table 3). The analysis of population diversities confirmed the impoverishment of the parasite community of *G. a. mahoratae* compared to *G. a. atlantica* (*G. a. atlantica* versus *G. a. laurae* $T_{27} = 0.17$, $p = 0.43$; *G. a. atlantica* versus *G. a. mahoratae* $T_{42} = 2.28$, $p = 0.01$; *G. a. laurae* vs. *G. a. mahoratae* $T_{27} = 1.52$, $p = 0.07$; false discovery rate-corrected).

Diet composition and variation

Table 1 shows the main descriptors of diet for the whole sample of each subspecies and Figure 3 displays the variation between classes. The plant component of the diet was considerable in all three subspecies (84.26% in *G. a. atlantica*, 61.24% in *G. a. laurae* and 73.03% in *G. a. mahoratae*), seeds, sprouts and flowers representing a substantial part. Nevertheless, the animal component was also quite diverse including 13 different taxa, among which Coleoptera, Formicidae, Heteroptera and Orthoptera were the most important depending on the subspecies. It must be remarked that cannibalism was detected in four cases, two in *G. a. atlantica* and two in *G. a. laurae*. Although no significant differences in the degree of herbivory were detected either across subspecies or between classes (two-way analysis of variance subspecies $F_{2,61} = 0.25$, $p = 0.78$; class $F_{3,61} = 1.58$, $p = 0.21$; subspecies * class $F_{4,61} = 0.25$, $p = 0.91$), adult females and especially immature lizards tended to include several

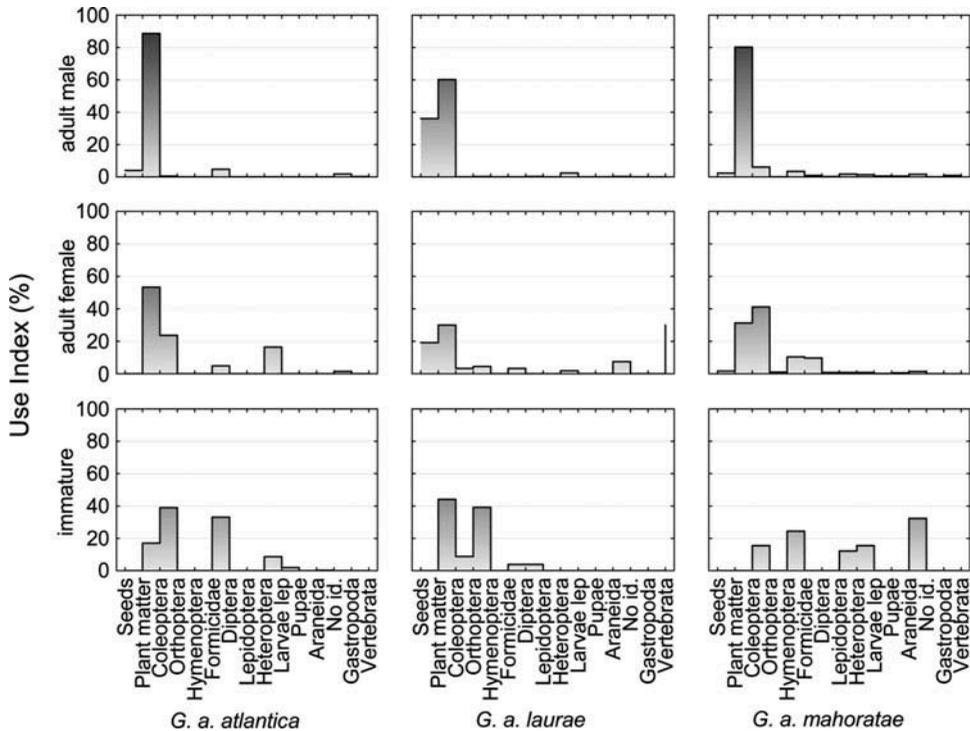


Figure 3. Variation in the diet of *Gallotia atlantica* considering the subspecies and class measured through the resource use index (Jover 1989; Carretero 2004).

animal taxa while *G. a. laurae* consumed more seeds than other plant elements (Figure 3).

The diversity parameters of diet pooled by subspecies are shown in Table 2. Of the four parameters considered, only individual diet diversity marginally correlated with lizard size ($r = -0.24$, $T_{69} = -2.04$, $p = 0.05$). As for the parasites, individual diversity attained values 7–10 times lower than population diversity for the three subspecies. When simultaneously comparing subspecies and classes (Table 3), juveniles carried more prey items than adults whereas prey richness, individual diversity and evenness were higher in *G. a. atlantica* than in the other two subspecies (Scheffé tests $p < 0.05$). Although the ontogenetic differences in abundance disappeared after accounting for body size, those for the other parameters remained across subspecies (Table 3). No differences in population diversity were found (t -tests, $p > 0.07$).

Host diet–parasite relationships

Helminth fauna and diet were associated at the individual level in *G. atlantica* (Table 4), albeit weakly. Such association appeared as a correlation between diet richness/diversity and parasite diversity/evenness, although only that between diet richness and parasite evenness remained significant after the correction for multiple tests (Table 4). Those analyses rendering significant results were repeated using

Table 4. Correlation matrix between parasite fauna and diet parameters in *Gallotia atlantica*.

Diet	Parasites			
	Abundance	Richness	Diversity	Evenness
Seeds	0.07 $p = 0.16$	0.13 $p = 0.27$	-0.05 $p = 0.66$	-0.05 $p = 0.67$
Other plant matter	0.04 $p = 0.77$	0.06 $p = 0.61$	<-0.01 $p = 1.00$	-0.01 $p = 0.93$
Total plant matter	0.04 $p = 0.72$	0.07 $p = 0.58$	<-0.01 $p = 0.98$	-0.01 $p = 0.91$
Abundance	0.12 $p = 0.31$	0.05 $p = 0.65$	-0.08 $p = 0.50$	-0.14 $p = 0.23$
Richness	-0.05 $p = 0.68$	0.10 $p = 0.40$	-0.29 $p = 0.01^*$	-0.32 $p = 0.005^{**}$
Diversity	0.01 $p = 0.95$	-0.03 $p = 0.77$	-0.24 $p = 0.04^*$	-0.26 $p = 0.03^*$
Evenness	0.08 $p = 0.49$	-0.04 $p = 0.77$	-0.16 $p = 0.17$	-0.18 $p = 0.12$

Notes: *Significant when considered separately. **Significant after applying the false discovery rate adjustment.

partial correlations of each parasite parameter with both diet and lizard size (not displayed). Once more, results indicated that only the partial correlations between the variables describing parasite community and diet were significant ($p < 0.03$) whereas the partial correlations between parasite variables and lizard size were not ($p > 0.52$).

Discussion

Helminth communities

Larval forms of cestodes were only found in the lizard hosts from Lanzarote. This suggests that lizards on this island may be intermediate or paratenic hosts in the life cycle of *Mesocestoides* sp., *Dipylidium* sp. and *Diplopylidium acanthotetra*, as has also been recorded for other Canarian lizards Martin and Roca 2004a, 2005; Martin et al. 2005). The absence of these larval forms in lizards from Fuerteventura suggests a lower predation pressure over *G. a. mahoratae* in the localities when they were captured. According to Martin and Roca (2005), feral cats are the most probable definitive hosts for these cestode larval forms and the presence, diversity and abundance of larval helminths depend on the overlap in the lizard range with local definitive hosts that eat lizards (Sharpilo et al. 2001). It is here suggested that the absence of mammal parasites in Fuerteventura is linked to the poor availability of definitive mammal hosts, when compared with Lanzarote. These findings are in accordance with the data provided by García-Márquez and Acosta (2003) showing low densities of feral cats in arid habitats of Fuerteventura.

Parasite prevalences approached, in some cases, those found in other *Gallotia* lizards (Martin et al. 2003, 2005; Martin and Roca 2004a, 2004b; Roca et al. 2005; Carretero et al. 2006). However, the helminth communities of *G. atlantica* were restricted to nine species, versus 12 in *Gallotia caesaris* and 13 in *Gallotia stehlini* (but only seven in *Gallotia galloti*, see previous references). This impoverishment was even more marked when the analysis was conducted at host subspecific level because no more than six were found in the same subspecies. Especially remarkable is the presence of only three species in *G. a. mahoratae* from Fuerteventura, all three of which were completely absent from *G. a. laurae* from northern Lanzarote. Although lizard densities are lower in

Fuerteventura than in Lanzarote (García-Márquez and Acosta 2003), this lack of redundancy, together with the endemicity of *Pseudoparadistomum yaizaensis* to *G. a. atlantica* suggest an influence of biogeographic factors in these parasite infracommunities. The species of the helminth infracommunities of *G. a. mahoratae* occurred more rarely than in the other host subspecies, and so *G. a. mahoratae* is closer to the typical pattern of helminth infection in many reptiles (Aho 1990; Roca and Hornero 1994; Martin and Roca 2005). The most recent phylogenetic analysis of *Gallotia* lizards (Cox et al. 2010) corroborates the ancient colonization of the Canary archipelago (around 20 million years ago) with Lanzarote and Fuerteventura, the oldest islands, now inhabited by *G. atlantica*, being the first colonized. It also indicates that the ancestors of *G. stehlini* from Gran Canaria and those of the species inhabiting the western islands were derived from two independent colonizations from the eastern islands, dated 11–13 million years and 9–10 million years ago, respectively (Cox et al. 2010). Finally, the coasts of Lanzarote and Fuerteventura were closer than nowadays during Pleistocene marine regressions, probably favouring lizard dispersal (Maca-Meyer et al. 2003; Cox et al. 2010), whereas the northern part of Lanzarote seems to have been isolated from the main range by Pleistocene volcanic events (Bloor et al. 2008). All this evidence suggests that vicariant and dispersal events of the host may have also left a biogeographic footprint in the pattern of helminth infracommunities. However, the influence of local ecological factors cannot be ignored (see below).

By contrast, the diversity pattern of the parasite communities was quite homogeneous in the hosts sampled. The influence of lizard size was weak but otherwise not uncommon in lacertids, and was explained by the increase of the probability of infection over the lifetime (see Sanchis et al. 2000; Martin et al. 2005; Carretero et al. 2011). A high ratio between populational and individual diversities derives from the heterogeneity of parasite communities between individual lizards. The variation between subspecies independent from lizard size was, nevertheless, the most remarkable finding. The helminth fauna of *G. a. mahoratae* appeared impoverished, especially regarding that of *G. a. atlantica*. Although insularity, either due to a “missing the boat” effect (MacLeod et al. 2010) or to the loss of alternative hosts after colonization (Roca et al. 2009), is a suitable hypothesis to explain this pattern, the influence of the arid conditions in Fuerteventura cannot be ruled out (see Diet).

Diet composition and variation

According to the proportion of plant matter consumed (73.03–84.26%), *G. atlantica* falls within the omnivorous lizards (Cooper and Vitt 2002), that is, this species is less close to pure herbivory within the herbivorous–carnivorous gradient (Roca 1999) than the large species *Gallotia simonyi* (Pérez-Mellado et al. 1999), *G. stehlini* (Carretero et al. 2006) and *G. galloti* (Valido and Nogales 2003; Roca et al. 2005). Instead it is closer in dietary habits to the small-sized *G. caesaris* (Martin et al. 2005). As in the latter, the herbivorous diet of *G. atlantica* tended to include the energetically richer seeds and fruits but also contained vegetative parts (leaves, stems). The animal fraction of the diet was diverse but common to many generalized lacertids (Carretero 2004), although consumption of ants and conspecifics, as found here, is usually restricted to insular lacertids (Pérez-Mellado and Corti 1993; Carretero et al. 2010).

Gallotia atlantica lacks the marked morphological specializations described for the large *Gallotia* species (tricuspid teeth, rectal caecum, Valido and Nogales 2003;

Herrel et al. 2004). However, the contribution of plant matter and the consumption of fibrous elements certainly exceed those reported for other insular lacertids of similar size. Other insular lacertids only consume plant reproductive parts (Pérez-Mellado and Corti 1993), while continental species remain almost strictly carnivorous (Carretero 2004). The combination of lack of terrestrial predators with high lizard densities and low arthropod availability seems to promote a trend towards trophic niche broadening on lacertids, namely to include plants in the diet (Pérez-Mellado and Corti 1993; Van Damme 1999; Carretero 2004). However, as *Gallotia* is the lineage with the longest evolution in insularity in lacertids and is also the only one displaying an extreme herbivore diet, this suggests that the evolutionary rate of such a trophic shift is slow (Carretero 2004).

A direct linkage between herbivory and lizard body size via morphological (space for large intestine) and physiological (low prey profitability) constraints was originally suggested by Pough (1973). Nevertheless, since then, numerous exceptions have been reported (King 1996; Vitt 2004; Espinoza et al. 2008). Also, many insular lizards, including *Gallotia* spp., may attain large body sizes (Meiri 2007; Novosolov et al. 2012) suggesting that insular herbivory could be mediated by body size at species level. However, large-scale comparative analyses indicated that the effects of insularity on body size and herbivory are largely independent (Van Damme 1999; Cooper and Vitt 2002). The results obtained here are in accordance with these findings. Being the smallest member of its genus, *G. atlantica* was certainly the least herbivorous (see above). However, it consumed more plants than other lacertids belonging to continental or recent insular lineages. Moreover, variation of herbivory between subspecies could not be attributed to body size and ontogenic variation within each population was weak.

Even if minor, the intraspecific variation in the diet found indicates some adaptive processes. Diet abundance was constrained by the gut size and, hence, displayed ontogenic variation that disappeared after correcting for body size (but see Valido and Nogales 2003). By contrast, diet complexity varied with the subspecies, which is here interpreted as derived from the richness of the local arthropod communities linked with humidity and vegetation (Pianka 1986). Also, the consumption of available plants according to their water content has been reported for other herbivorous lizards (Rocha 2000; Dutra et al. 2011). Significantly, the diet of *G. a. mahoratae* inhabiting the arid Fuerteventura was the least diverse. Moreover, the diet diversity was much higher for populations than for individuals, indicating a strong degree of interindividual variation (Carretero et al. 2001), especially regarding the animal component of the diet.

Host diet–parasite relationships

According to Petter and Quentin (1976), the nematodes of the family Pharyngodonidae are indicative of the feeding habits of the reptile hosts. The genera *Parapharyngodon*, *Parathelandros*, *Pharyngodon*, *Skrjabinodon* and *Spauligodon* belong to an evolutionary lineage parasitizing carnivorous saurians, whereas *Alaeuris*, *Mamillomacracis*, *Mehdiella*, *Ortleppnema*, *Ozolaimus*, *Tachygonetria*, *Thaparia* and *Travassozolaimus* parasitize both herbivore iguanids and tortoises. In this context, the intestinal helminth community of *G. atlantica* deviates from those found in other Canarian lacertids, including the small and omnivorous *G. caesaris*

(Martin and Roca 2004a, 2005; Martin et al. 2005). These western host species harbour more Pharyngodonidae of the herbivorous lineage (never found in other Palearctic insular or continental lacertids, Roca 1999) and fewer Pharyngodonidae of the carnivorous lineage. By contrast, the Pharyngodonidae found in *G. atlantica* belonged exclusively to the genera *Parapharyngodon* and *Spauligodon*, typical of carnivorous lizards whereas the nematodes belonging to the herbivorous lineage were lacking. Although nematodes of other families like *Skrjabinelazia* sp. found here also appear in herbivorous lizards, this finding agrees with the less accentuated trend to herbivory detected in the diet analysis. *Skrjabinelazia* sp. might have colonized the other *Gallotia* species later, eventually coming through the sympatric *Tarentola* geckos (Roca et al. 1999), after the separation from the *G. atlantica* ancestor, hence, leaving it absent from the eastern islands.

Finally, the association found between the complexity of helminth communities and diet deserves special comment, because it has already been reported for *G. caesaris* (Martin et al. 2005), *G. galloti* (Roca et al. 2005) and *G. stehlini* (Carretero et al. 2006). Indeed, lizard populations or species could acquire helminth faunas and diets due to common causative factors (i.e. a common biogeography or habitat dependence) rather than as a result from direct association between both traits. However, detection of a parasite–diet correlation at an individual level in different *Gallotia* species and populations together with its independence from the host size, strongly suggest that functional relationships between parasites and prey items ingested are taking place inside the digestive tract (Roca 1999). The nature of such processes should be formally evaluated not only through comparative analyses across the whole genus considering its phylogeny and distribution but especially by means of experimental infestation/removal of nematodes (Wadding et al. 2004).

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