

## Relationship between diet and helminths in *Gallotia caesaris* (Sauria: Lacertidae)

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### Abstract

Diet and helminth fauna were analysed in *Gallotia caesaris*, a small lacertid lizard endemic to El Hierro (Canary Islands, Spain) in order to study the evolutionary and functional relationships between the two traits. This species is omnivorous but consumed a high proportion (82.13%) of plant matter including not only seeds but also leaves and other vegetative parts. Helminth fauna included many helminth species typical of herbivorous reptiles. Both herbivory and helminth presence were higher than expected for a lizard of its size. Comparison with other lacertids suggests that both traits result from an adaptation to insular conditions but that some “evolutionary time” to develop them is needed. Canarian *Gallotia* lizards, a separate lineage evolving for a long time in insularity, constitutes the most advanced lacertid group in this way. Nevertheless, results for *G. caesaris* indicate that helminth fauna also changes seasonally tracking variation in diet (and herbivory) throughout the year, which suggests a dynamic interaction between diet and helminth parasites.

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**Keywords:** Helminth community; Diet–parasite relationship; Diet composition; Island ecosystems

### Introduction

The recruitment of many parasites depends on the feeding habits of their hosts (e.g. Bush, 1990). This is evident in heteroxenous parasites, but also occurs in many helminths with direct life cycles. At least in

reptiles, carnivory or herbivory of hosts results in important differences in their respective helminth faunas (Petter and Quentin, 1976; Roca, 1999). Two main differences have been noted in the literature, (i) infection by distinct species of nematodes; Petter and Quentin (1976) recognised two evolutionary lineages within the family Pharyngodonidae parasitising carnivorous and herbivorous reptiles; (ii) the structure of helminth communities, which are more rich and diverse in

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herbivorous than in carnivorous reptiles (Aho, 1990; Roca and Hornero, 1991).

The family Lacertidae comprises close to 300 species of lizards found mainly in the Old World with diet regimes ranging from strict carnivory (insectivory) to herbivory, the latter usually found in ancient insular lineages. Recently, the relationship between helminth communities and consumption of plant matter by reptiles has been examined in insular lacertids, including both omnivorous (*Podarcis*) and omnivorous and herbivorous (*Gallotia*) species (Roca and Hornero, 1991; Roca, 1999; Roca et al., 2005). The results of these studies suggest that consumption of different types of plant matter (seeds, pollen or fibre) is associated with distinct helminth faunas (Roca, 1996).

Species or populations of lacertids living on islands show a higher tendency towards herbivory than their counterparts on the mainland (Sadek, 1981; Van Damme, 1999) and, when evolutionary history under insular conditions is long enough, true specialisations involving anatomy and behaviour have been demonstrated (Bischoff, 2000; Carretero et al., 2001; Carretero, 2004; Herrel et al., 2004), associated with a great infection by nematode parasites (Dearing, 1993). The genus *Gallotia* constitutes an early separated branch of lacertids (Harris et al., 1998) endemic to the Canary Islands where they evolved and diversified in insularity for more than 12 million years (Carranza, 2002). Since all extant members of this genus consume plant matter in different degrees (Roca, 1999), they can be useful for detailed studies of host diet–parasites relationships.

In this study, we report data of diet and helminth parasites of Boetger's lizard *Gallotia caesaris* (Lehrs, 1914). The subspecies *G. c. caesaris* is a small to medium-sized lacertid lizard living on the island of El Hierro (Mateo and García-Márquez, 2002). A general description of its helminth communities has recently been published (Martin et al., 2003) and their infra-communities and component communities have been analysed (Martin and Roca, 2004a). However, little is known about the diet of this species (Machado, 1985; Roca, 1999) and consequently, diet–parasite relationships of this lacertid lizard have not been assessed. Hence, the aim of this paper is to investigate the relationship between helminth and diet parameters of *G. caesaris*, specifically addressing the following issues: (i) characterisation of the patterns of helminth community richness and diversity; (ii) characterisation of the patterns of dominance and diversity in the diet; (iii) analysis of the sexual and seasonal variation of diet and parasites; (iv) determination of relationships between helminths and diet. Additionally, we aimed to test two general predictions concerning the relationship between helminth parasites and diet. First, since *G. caesaris* belongs to an old insular lineage, we expect that it should harbour complex herbivorous helminth faunas

(including some species typical of herbivorous reptiles). Second, at the functional level, we predict that if diet complexity and the degree of herbivory vary seasonally then the complexity of the helminth fauna should respond to this change.

## Materials and methods

### Animals and collection localities

Lizards were collected on El Hierro, the westernmost island of the Canarian Archipelago, located off the northwest coast of Africa (27° 37'–29° 24'N and 13° 37'–8° 10'W). El Hierro is a volcanic island (269 km<sup>2</sup>; 1500 m maximum elevation) microclimatically and ecologically heterogeneous, due to the interaction of its orography with wet air masses carried by trade winds, and the presence of ancient volcanic soils that provide multiple opportunities for plant colonisation (García-Márquez et al., 1999b). A total of 196 adult specimens of *G. c. caesaris*, 73 males, 109 females, and 14 not sexed; 73 in spring (May–June), 63 in summer (July and September), 29 in autumn (October–November), 24 in winter (February–March) and 6 undated, were collected by hand in the localities of Dehesa and Guinea in 1995. The habitat in both localities was similar, typically found at low altitude, dominated by volcanic rocks and scattered bushes and called “malpaís” (badlands).

### Sampling of hosts

Lizards were transported to the laboratory, sacrificed with an overdose of chloroform and processed immediately. Snout vent length (SVL) was measured with a digital calliper to the nearest 0.01 mm. Digestive tracts were removed and the stomach contents were used for diet description. The minimum number criterion was used for prey counting (Escarré and Vericad, 1981; Carretero and Llorente, 1993). With some exceptions, the order level was used as operational taxonomic unit (OTU), (Sneath and Sokal, 1973) for identification (see Table 1). In 142 of 196 lizards, rectum contents were analysed helminthologically under a binocular dissecting microscope. Helminths were counted, washed in distilled water, fixed, mounted using standard techniques (for details see Roca, 1985), and identified to species.

### Statistical analyses

The descriptors of diet and parasite fauna were the prevalence (percentage of lizards with prey/parasite items); the abundance (percentage of each prey or

**Table 1.** Descriptors of parasite fauna and diet of *Gallotia caesaris*

OTUs	Total				Males				Females			
	<i>N</i>	% <i>P</i>	% <i>N</i>	IU	<i>N</i>	% <i>P</i>	% <i>N</i>	IU	<i>N</i>	% <i>P</i>	% <i>N</i>	IU
<b>Diet</b>												
Seeds	1020	48.53	42.95	38.47	264	53.33	33.38	27.41	721	48.15	48.68	43.90
Coleoptera	103	54.41	4.34	4.59	39	60.00	4.93	5.52	63	56.79	4.25	4.50
Orthoptera	13	9.56	0.55	0.36	5	11.11	0.63	0.36	7	8.64	0.47	0.27
Diptera	72	43.38	3.03	3.10	23	40.00	2.91	2.86	46	46.91	3.11	3.23
Araneae	25	16.18	1.05	0.82	8	17.78	1.01	0.75	17	17.28	1.15	0.86
Formicidae	203	53.68	8.55	8.48	69	60.00	8.72	8.59	122	49.38	8.24	8.01
Larvae	18	6.62	0.76	0.35	10	13.33	1.26	0.54	7	2.47	0.47	0.09
Miriapoda	2	1.47	0.08	0.02	1	2.22	0.13	0.00	1	1.23	0.07	0.00
Pupae	8	4.41	0.34	0.15	3	4.44	0.38	0.08	5	4.94	0.34	0.13
Vertebrata	1	0.74	0.04	0.00	1	2.22	0.13	0.00	0	—	—	—
Gastropoda	1	0.74	0.04	0.00	0	—	—	—	1	1.23	0.07	0.00
Other plant matter	909	93.38	38.27	43.66	368	95.56	46.52	53.89	491	93.83	33.15	39.01
<b>Parasites</b>												
<i>Th. galloti</i>	1956	43.02	37.59	35.88	462	43.28	17.85	23.84	561	52.08	23.61	32.88
<i>Th. filiformis</i>	195	6.40	3.75	3.08	1089	26.87	42.08	30.24	451	22.92	18.98	12.31
<i>Th. tinerfensis</i>	959	24.42	18.43	20.56	0	—	—	—	81	4.17	3.41	1.87
<i>S. atlanticus</i>	1052	30.23	20.22	21.77	929	52.24	35.90	42.30	868	39.58	36.53	45.48
<i>P. micipsae</i>	112	10.47	2.15	1.91	74	16.42	2.86	2.62	121	23.96	5.09	5.83
<i>A. numidica</i>	31	0.58	0.60	0.00	3	1.49	0.12	0.00	15	1.04	0.63	0.00
<i>T. dentata</i>	33	0.58	0.63	0.00	0	—	—	—	31	1.04	1.31	0.00
<i>T. macrolaimus</i>	42	13.95	0.81	0.74	0	—	—	—	33	1.04	1.39	0.00
<i>S. pyrenaica</i>	20	6.98	0.38	0.30	19	19.40	0.73	0.79	40	20.83	1.68	1.57
<i>Centrorhynchus</i> sp.	1	0.58	0.02	0.00	1	1.49	0.04	0.00	0	—	—	—
<i>Mesocestoides</i> sp.	178	2.91	3.42	0.10	0	—	—	—	171	1.04	7.20	0.00
Spirurida gen. sp.	624	30.81	11.99	15.65	11	5.97	0.43	0.20	4	3.13	0.17	0.07

*N*: total number of prey items (intensity); %*P*: percent occurrence (prevalence); %*N*: percent abundance; IU: resource use index (Jover, 1989; Carretero, 2005).

parasite item); and the resource use index (Jover, 1989) which emphasises the homogeneity as a criterion for evaluating the importance of the different OTUs (see Carretero and Llorente, 1993; Carretero et al., 2001; Carretero, 2004). The use of descriptive eco-parasitological terms followed Bush et al. (1997).

Overall parameters of both helminth infracommunities and diet for the whole population as well as separated by sex and season were calculated as mean individual values and compared by means of ANCOVA. Since most of the variables were size-dependent (see below), SVL was used as a covariate in the analyses. Variables were log-transformed in order to reach normality (assessed by Kolmogorov–Smirnov tests). Helminth infracommunities and diet were compared statistically by means of the following parameters: abundance (number of helminths or prey items), richness (number of parasite species or OTUs), diversity and evenness. Brillouin's indices were used for calculating diversity and evenness according to Magurran (2004). For diet, population diversity (Hp) was also estimated by the jack-knife technique (Carretero, 2004) and compared by multiple *t* tests due to the non-additive

nature of diversity (Carretero and Llorente, 1991, 1993) and then applying the sequential Bonferroni correction (Rice, 1989).

## Results

Body size of *G. caesaris* from El Hierro was relatively small (SVL =  $67.2 \pm 0.6$  mm, unsexed individuals included) and showed no sexual dimorphism (males  $68.4 \pm 0.9$  mm, range 50–85 mm; females  $67.3 \pm 0.7$  mm, range 49–83 mm;  $t_{180} = 0.98$ ,  $p = 0.33$ , n.s.).

## Diet composition and variation

Table 1 shows the main diet descriptors pooled for the whole population and separated by sexes. *G. caesaris* was mainly herbivorous (82.13% plant matter). Leaves were the most important plant item but seeds were also abundant, especially in spring (Fig. 1). Animal matter was very diverse including prey belonging to 10 different taxa, Formicidae, Coleoptera and Diptera being the

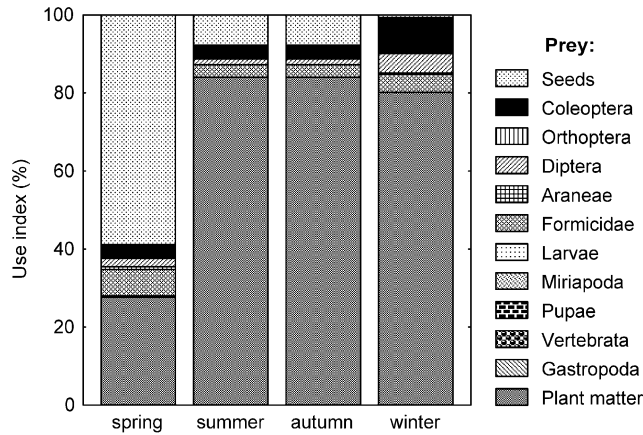


Fig. 1. Seasonal variation of the diet of *G. caesaris*.

most important. The contribution of all three to the whole diet was limited but increased considerably in winter (Fig. 1).

The degree of herbivory did not change with sex but varied seasonally, being less pronounced in winter (2 way-ANOVA, factor sex  $F_{1,119} = 0.006$ ,  $p = 0.94$ , n.s.; factor season  $F_{3,119} = 11.60$ ,  $p = 10^{-6}$  ( $<0.001$ ); interaction  $F_{3,119} = 0.39$ ,  $p = 0.76$ , n.s.). Eight digestive tracts, corresponding to all seasons and both sexes, had no prey content.

Both diet abundance and richness were correlated with body size (both log-transformed; abundance  $R^2 = 0.10$ ,  $p = 0.0001$ ; richness  $R^2 = 0.08$ ,  $p = 0.0007$ ). The overall diversity parameters of diet are indicated in Table 2. Individual diversity was lower than population diversity in all cases, although the differences were small (Fig. 2). Although no significant differences between sexes were found for any of the parameters, seasonal variation was important for all of them (Table 3). Prey abundance and richness were higher in spring than during the rest of the year. However, individual diversity was higher in autumn (followed by spring) whereas evenness was low in winter. There was no correlation between individual diversity and evenness. Population diversity showed similar trends, with higher values in autumn than in other seasons (see Tables 2 and 3).

**Helminth communities**

A total of 12 different helminth species were found in *G. caesaris*. The acanthocephalan *Centrorhynchus* sp., the cestode *Mesocestoides* sp. and the nematode *Spirurida* gen. sp., were larval forms found in the body cavity of the hosts. The nematode *Skrjabinelazia pyrenaica* was found in the stomach. The intestinal helminth component community of *G. caesaris* was composed exclusively of nematodes of the family Pharyngodonidae, all of them living in the lower portion

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

	Parameter	N	Total mean ± SE (range)
Parasites	Abundance	196	26.55 ± 3.38 (0–350)
	Richness	196	1.50 ± 0.07 (0–5)
	Indiv. diversity	196	0.30 ± 0.03 (0–1.59)
	Pop. diversity	—	2.54 ± 0.17 (Jack-knife)
	Evenness	196	0.21 ± 0.02 (0–1.10)
	Diet	Abundance	142
Richness		142	3.19 ± 0.13 (0–7)
Indiv. diversity		135	0.77 ± 0.05 (0–1.93)
Pop. diversity		—	1.92 ± 5.27 (Jack-knife)
Evenness		121	0.47 ± 0.02 (0–1.59)

of the intestine (rectum). Prevalence, intensity of infection and abundance for each helminth species pooled for the whole population and separated by sexes, are shown in Table 1. *Thelandros galloti*, *Th. tinerfensis*, *Spauligodon atlanticus* and *Tachygonetria macrolaimus* were the most important parasites of the component community of *G. caesaris*.

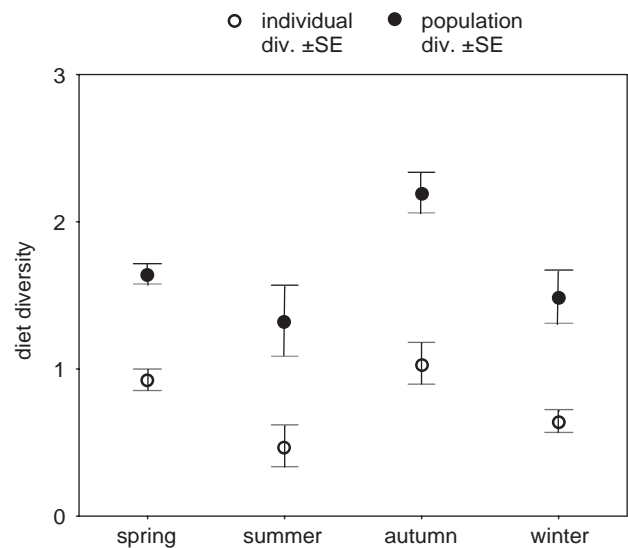


Fig. 2. Seasonal variation of prey individual and populational diversity of *G. caesaris*.

**Table 3.** ANOVA (and *T*) comparisons for the abundance, richness and diversity of parasite species, and the same parameters of the diet of lizards (size-corrected)

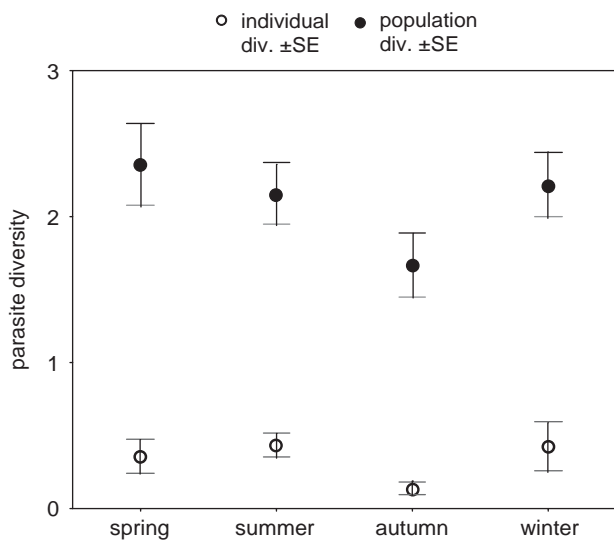
	Parameter	Sex		Season		Interaction	
		<i>F</i> <sub>d.f.</sub>	<i>P</i>	<i>F</i> <sub>d.f.</sub>	<i>P</i>	<i>F</i> <sub>d.f.</sub>	<i>P</i>
Parasites	Abundance	$F_{1,167} = 2.06$	0.15	$F_{3,167} = 0.54$	0.65	$F_{3,167} = 0.96$	0.41
	Richness	$F_{1,167} = 0.34$	0.56	$F_{3,167} = 0.40$	0.75	$F_{3,167} = 0.55$	0.64
	Indiv. diversity	$F_{1,167} = 0.01$	0.92	$F_{3,167} = 1.70$	0.16	$F_{3,167} = 0.53$	0.66
	Pop. diversity	$T_{44} = 2.36$	0.01	Mult. <i>T</i>	<sup>a</sup>	—	—
	Evenness	$F_{1,167} = 0.01$	0.92	$F_{3,167} = 1.72$	0.16	$F_{1,167} = 0.57$	0.53
Diet	Abundance	$F_{1,119} = 0.39$	0.53	$F_{3,119} = 12.72$	$2.87 \times 10^{-7}$	$F_{3,119} = 0.31$	0.81
	Richness	$F_{1,119} = 1.85$	0.17	$F_{3,119} = 15.00$	$2.41 \times 10^{-8}$	$F_{3,119} = 0.58$	0.63
	Indiv. diversity	$F_{1,116} = 3.20$	0.07	$F_{3,116} = 17.69$	$1.6 \times 10^{-9}$	$F_{3,116} = 0.68$	0.56
	Pop. diversity	$T_{44} = 0.83$	0.20	Mult. <i>T</i>	<sup>b</sup>	—	—
	Evenness	$F_{1,105} = 0.99$	0.32	$F_{3,105} = 9.85$	$8.79 \times 10^{-6}$	$F_{3,119} = 0.81$	0.49

<sup>a</sup>Spring–summer:  $T_{89} = 0.54$ ,  $p = 0.30$ , n.s.; spring–autumn:  $T_{81} = 1.85$ ,  $p = 0.03$ , spring–winter:  $T_{45} = 0.37$ ,  $p = 0.36$ , n.s.; summer–autumn:  $T_{118} = 1.60$ ,  $p = 0.06$ , n.s.; summer–winter:  $T_{82} = 0.15$ ,  $p = 0.44$ , n.s.; autumn–winter:  $T_{74} = 1.40$ ,  $p = 0.08$ , n.s.

<sup>b</sup>Spring–summer:  $T_{80} = 1.72$ ,  $p = 0.04$ ; spring–autumn:  $T_{85} = 3.92$ ,  $p = 8 \times 10^{-5}$ ; Spring–winter:  $T_{80} = 1.01$ ,  $p = 0.15$ , n.s.; summer–autumn:  $T_{49} = 3.27$ ,  $p = 0.001$ ; summer–winter:  $T_{45} = 0.54$ ,  $p = 0.30$ , n.s.; autumn–winter:  $T_{50} = 3.16$ ,  $p = 0.001$ .

There were some differences in the presence of parasites in males and females of *G. caesaris*. *Th. tinerfensis*, *Tachygonetria dentata* and *T. macrolaimus* were present in the digestive tract of females but not in males, although their prevalences were low (Table 1). There were no significant differences in the abundance and richness of helminths for different seasons.

Both species richness and abundance of parasites were weakly correlated with body size (both log-transformed; abundance  $R^2 = 0.03$ ,  $p = 0.02$ ; richness  $R^2 = 0.02$ ,  $p = 0.03$ ). Table 2 shows the diversity parameters of the nematode infracommunities of the hosts. As in the case of diet, individual diversity was lower than population diversity in all cases (Fig. 3).

**Fig. 3.** Seasonal variation of helminth individual and population diversity of *G. caesaris*.

## Host diet–parasite relationships

Helminth fauna and diet were associated in *G. caesaris* at the individual level. When considering the whole sample, parasite richness, diversity and evenness were correlated with the evenness of the diet (Table 4). However, when analysed separately by seasons, correlations remained statistically significant (and extended to parasite abundance and diet diversity) only for the winter sample (Table 4). None of these differences could be associated specifically with plant matter consumption at the individual level.

## Discussion

### Diet composition and variation

Lizards are usually considered herbivorous when they eat more than 90% plant matter, and strictly herbivorous species tend to be folivorous. Adaptations for processing leaves have been described in *Gallotia* lizards, including specialised dentition, elongated intestines, mechanisms slowing food passage, and intestinal flora that digest cellulose (Pérez-Mellado et al., 1999; Herrel et al., 2004; Carretero, 2004). Omnivorous lizards lacking such specialisations may eat some leaves but more often consume other plant parts, such as seeds, flowers, or fruits (Cooper and Vitt, 2002). The genus *Gallotia* as a whole has been considered as omnivorous (Barbadillo et al., 1999) and consumption of different plant parts, such as nectar, seeds, pollen and leaves has been reported in some species (Font and Ferrer, 1995; Pérez-Mellado et al., 1999).

**Table 4.** Correlation matrix between the overall parameters of diet and parasite fauna

		Abund. diet	Richness diet	Diversity diet	Evenness diet
Total <i>n</i> = 121	Abund. parasites	−0.20 <i>p</i> = 0.03*	−0.15 <i>p</i> = 0.10	0.02 <i>p</i> = 0.85	0.10 <i>p</i> = 0.30
	Richness parasites	−0.18 <i>p</i> = 0.04*	−0.15 <i>p</i> = 0.10	0.14 <i>p</i> = 0.12	0.29 <i>p</i> = 0.001**
	Diversity parasites	−0.16 <i>p</i> = 0.09	−0.19 <i>p</i> = 0.04*	0.12 <i>p</i> = 0.20	0.31 <i>p</i> = 0.001**
	Evenness parasites	−0.15 <i>p</i> = 0.08	−0.19 <i>p</i> = 0.04*	0.12 <i>p</i> = 0.20	0.31 <i>p</i> = 0.001**
Spring <i>n</i> = 57	Abund. parasites	−0.10 <i>p</i> = 0.46	−0.21 <i>p</i> = 0.11	−0.17 <i>p</i> = 0.21	−0.11 <i>p</i> = 0.43
	Richness parasites	−0.07 <i>p</i> = 0.62	−0.18 <i>p</i> = 0.19	−0.06 <i>p</i> = 0.68	0.07 <i>p</i> = 0.59
	Diversity parasites	−0.05 <i>p</i> = 0.81	−0.03 <i>p</i> = 0.67	0.03 <i>p</i> = 0.82	0.11 <i>p</i> = 0.44
	Evenness parasites	−0.06 <i>p</i> = 0.68	−0.03 <i>p</i> = 0.83	0.04 <i>p</i> = 0.80	0.11 <i>p</i> = 0.43
Summer <i>n</i> = 14	Abund. parasites	−0.35 <i>p</i> = 0.22	−0.39 <i>p</i> = 0.16	−0.29 <i>p</i> = 0.31	−0.05 <i>p</i> = 0.87
	Richness parasites	−0.18 <i>p</i> = 0.54	−0.49 <i>p</i> = 0.08	−0.46 <i>p</i> = 0.10	−0.21 <i>p</i> = 0.46
	Diversity parasites	0.02 <i>p</i> = 0.95	−0.51 <i>p</i> = 0.06	−0.55 <i>p</i> = 0.04*	−0.35 <i>p</i> = 0.22
	Evenness parasites	0.01 <i>p</i> = 0.98	−0.51 <i>p</i> = 0.06	−0.55 <i>p</i> = 0.04*	−0.34 <i>p</i> = 0.23
Autumn <i>n</i> = 26	Abund. parasites	0.01 <i>p</i> = 0.95	0.29 <i>p</i> = 0.15	0.24 <i>p</i> = 0.23	−0.03 <i>p</i> = 0.88
	Richness parasites	−0.008 <i>p</i> = 0.97	0.24 <i>p</i> = 0.24	0.19 <i>p</i> = 0.35	−0.06 <i>p</i> = 0.79
	Diversity parasites	−0.03 <i>p</i> = 0.98	−0.26 <i>p</i> = 0.19	−0.04 <i>p</i> = 0.83	−0.08 <i>p</i> = 0.69
	Evenness parasites	−0.02 <i>p</i> = 0.90	−0.26 <i>p</i> = 0.20	−0.04 <i>p</i> = 0.84	−0.07 <i>p</i> = 0.70
Winter <i>n</i> = 23	Abund. parasites	−0.27 <i>p</i> = 0.74	−0.12 <i>p</i> = 0.37	0.42 <i>p</i> < 0.001**	0.41 <i>p</i> < 0.001**
	Richness parasites	0.19 <i>p</i> = 0.37	−0.07 <i>p</i> = 0.74	0.86 <i>p</i> < 0.05*	0.83 <i>p</i> < 0.05*
	Diversity parasites	−0.01 <i>p</i> = 0.95	−0.11 <i>p</i> = 0.62	0.99 <i>p</i> < 0.001**	0.97 <i>p</i> < 0.001**
	Evenness parasites	−0.01 <i>p</i> = 0.95	−0.11 <i>p</i> = 0.63	0.99 <i>p</i> < 0.001**	0.97 <i>p</i> < 0.001**

\*Significant when considered isolatedly.

\*\*Significant after applying sequential Bonferroni adjustment.

Body size is an important factor that was thought to be closely linked to plant consumption by lizards (Cooper and Vitt, 2002). Although Pough (1973) stated that herbivorous lizards tend to be >300 g, many smaller species have been reported eating plants (Schluter, 1984; King, 1996). Nevertheless, herbivory in lizards is still roughly associated with large body size, and this also applies to lacertid lizards (Van Damme, 1999). The results of Cooper and Vitt (2002) for lizards support the hypothesis that increased body size is a consequence of plant consumption. Although there seem to be no physiological or structural reasons for a herbivorous lizard to be large (King, 1996), some ecological reasons have been put forward (Mautz and Nagy, 1987). Van Damme (1999) concluded that large body size in lacertids would be a by-product of insularity but not a factor directly promoting herbivory. This seems to fit with the results observed in the Canarian medium-sized *Gallotia*. On the Canary Islands, Valido and Nogales (2003) stated that there are different degrees of herbivory among distinct species and populations of *G. galloti* from Tenerife, and *G. atlantica* from Fuerteventura. Neither of these two species present any specific digestive or physiological adaptations to herbivory other than body size, and thus were considered omnivorous. *G. simonyi*, a giant lizard that is also found on El Hierro, has been considered basically herbivorous, with a tendency to omnivory,

although the only evidence of adaptation to herbivory reported for this lizard is a rich fauna of intestinal nematodes (Roca et al., 1999) and the presence of three cusps per tooth (López-Jurado, 1989; Mateo et al., 1999). Although our results show that *G. caesaris* is omnivorous, the consumption of leaves and the presence of a particular intestinal nematode fauna (see below) indicates a strong tendency to herbivory. In fact, considering the size of *G. caesaris* (67.2±0.6 mm), intermediate between *G. atlantica* (60.5 mm) and *G. galloti* (119–95.7 mm; data from Valido and Nogales, 2003), its degree of herbivory (82.13% plant matter) is much higher than expected (28.3% in *G. atlantica* and 20.6–80.9% in *G. galloti*, respectively, Valido and Nogales, 2003). This supports the idea that small Canarian lacertid lizards seem likely to develop the same strong tendency to herbivory as large species do, and suggests that factors other than body size (i.e. phylogenetic) are also responsible for herbivory (Carretero, 2004).

Seasonal variability in prey consumption can be explained in terms of changes in food availability. Llorente et al. (1999) and Orrit et al. (1999) provided reliable estimations of animal and plant availability, respectively, in our study areas. The low consumptions of plant matter by *G. caesaris* in winter, and seeds in winter and autumn are associated with the absence of plant reproduction in those seasons (Orrit et al., 1999).

Moreover, animal and plant availability are higher in spring than during the rest of the year (Llorente et al., 1999; Orrit et al., 1999), and this is reflected in the prey abundance and richness in the gut contents. However, seasonal variation in diversity (which reflects variation in both evenness and richness) apparently does not only depend on food availability (Carretero, 2004). Thus, whereas in spring high diversity mainly derives from the balanced representation of seeds and other plant matter in the diet, in autumn it is the result of the inclusion of animals in the diet since the plant fraction is almost exclusively composed of leaves and tiles. The relatively small differences between individual and population diversity reveal reduced diet differences between individuals in comparison with other lacertids (Carretero and Llorente, 1991, 1993; Carretero et al., 2001) and result from the fact that the number of prey items consumed by individuals is high in comparison with insectivorous species.

Some other factors might affect the evolution of plant consumption, insularity being one of the most important (Cooper and Vitt, 2002). Van Damme (1999) found that insular lacertids eat more plant matter than those on the mainland, and Cooper and Vitt (2002) found a highly significant correlated evolution of insularity and omnivory in Lacertiformes. More specifically, lower prey availability and high density on islands might be a major force for broadening of the diet to include plants (Pérez-Mellado and Corti, 1993). Simultaneously, reduced predator pressure in island ecosystems might allow prolonged digestion of plants (Van Damme, 1999). Both low prey availability and lack of native predators may explain the results obtained with *G. caesaris*. Thus, Llorente et al. (1999) found that both number of animal prey and biomass available were scarce throughout the year on El Hierro. The Canary Islands have no native terrestrial predators that could predate on these endemic lizards. Cejudo et al. (1999) and García-Márquez et al. (1999b) only found (introduced) feral cats and kestrels (*Falco tinnunculus*) as predators of *G. caesaris*.

### Helminth communities

The presence of larval forms of helminths infecting *G. caesaris* suggests that this lizard may be an intermediate and/or paratenic host in the life cycles of *Mesocestoides* sp., *Centrorhynchus* sp., and Spirurida gen. sp. (Martin and Roca, 2004a). It is consistent with reports of Martin and Roca (2005) who described a similar situation for *G. atlantica* on the island of Lanzarote.

A correlation between host body size and richness and abundance of helminths is common in lizards. Roca et al. (1990) pointed out that this situation is simply a consequence of the increased opportunities for older individuals to acquire an infection compared to younger

ones; and also a consequence of more opportunities for contacts among adults due to mating and territorial fights. Contacts among adults of *G. caesaris* are favoured on the island of El Hierro by high population densities (García-Márquez et al., 1999a).

Usually, host sex has no influence on the composition and structure of helminth communities of lizards. As in our study (see Results), small sex-related differences were observed in some lizard species like *L. schreiberi*, but not in some others like *Podarcis hispanica*, *Lacerta lepida* or *Acanthodactylus erythrurus* (Roca et al., 1990). These differences were explained by the different feeding behaviour of males and females. Seasonality had no effect on the infection of *G. caesaris* by helminths, in accordance with results obtained from the study of other reptile hosts (Burseley and Goldberg, 1991; Sanchis et al., 2000); it seems that only rainfall can influence infection of reptile hosts in rainforest habitats (Rocha, 1995; Sanchis et al., 2000).

### Host diet–parasite relationships

The intestinal helminth community of *G. caesaris* is in accordance with the typical pattern found in other Canarian lacertids, in which Pharyngodonidae nematodes are the most common helminths (Martin and Roca, 2004a,b, 2005; Roca et al., 2005).

Among these Pharyngodonidae nematodes, *Gallotia* lizards harbour some species that belong to the evolutionary lineage reported from herbivorous reptiles (see Introduction and References below) but have never been found in other Palaeartic insular or continental lacertid lizards (Roca, 1999). *G. caesaris* harboured six of these species, *Th. galloti*, *Th. filiformis*, *Th. tinerfensis*, *A. numidica*, *T. dentata*, and *T. macrolaimus*, and only two, *S. atlanticus* and *P. micipsae*, belonging to the lineage known from carnivorous reptiles. This is again consistent with an important degree of herbivory of *G. caesaris* as shown by the analysis of its diet (Table 1).

The tendency to herbivory has been reported in other insular lacertids (Van Damme, 1999), e.g. *Podarcis lilfordi* and *P. pityusensis* from the Balearic Islands (Pérez-Mellado and Corti, 1993; Roca and Hornero, 1994). Balearic *Podarcis* colonised their islands later than *Gallotia* (7–5 million years, Alcover et al., 1981), exhibit pseudo-specialisation (without physiological and with minimal morphological changes) sometimes leading to a temporary stenophagy, and high consumption of vegetable matter, mainly the most energetic parts of plants such as pollen and seeds (Pérez-Mellado and Corti, 1993). Their helminth faunas are typical of carnivorous reptiles (Roca and Hornero, 1994). This suggests that Balearic lacertids are primarily carnivorous showing a partial herbivory considered as an adaptive response related to the trophic availability

and to the evolutionary age of the lizard population on each island (Roca, 1996). In contrast, Canarian *Gallotia* constitute a much older insular lineage (more than 12.6 million years, Carranza, 2002) clearly separated from other lineages in the lacertid phylogeny (Harris et al., 1998). Moreover, their consumption of plant matter includes not only plant reproductive organs but also vegetative matter such as leaves (see Results and Valido and Nogales, 2003 and own data). In addition, parasitological features corroborate the tendency of *Gallotia* lizards to herbivory (Roca and Hornero, 1991; Roca et al., 2005): (i) absence of 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.

This evidence suggests that, although *G. caesaris* is similar in size to *Podarcis* species from the Balearic Islands and faces equivalent insular conditions (high density, low terrestrial predation and low availability of animal prey), it has progressed in the specialisation to herbivory. Nevertheless, such specialisation is neither static nor absolute since helminth fauna changes seasonally paralleling variation of diet (and herbivory) throughout the year. Although relationships between parasites and diet were weak (<10% variance explained), results are consistent with those found in *G. galloti* (Roca et al., 2005) suggesting dynamic interactions between these two parameters. This aspect should be subject to further research.

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## References

Aho, J.M., 1990. Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes. In: Esch, G., Bush, A.O., Aho, J. (Eds.),

- Parasite Communities: Patterns and Processes. Chapman & Hall, London, pp. 157–195.
- Alcover, J.A., Moyà-Solà, S., Pons-Moyà, J., 1981. Les Quimeres del Passat. Els Vertebrats Fòssils del Plioc-Quaternari de les Balears i Pituisès. Moll, Mallorca.
- Barbadillo, L.J., Lacomba, I., Pérez-Mellado, V., Sancho, V., López-Jurado, L.F., 1999. Anfibios y Reptiles de la Península Ibérica, Baleares y Canarias. Geoplaneta, Barcelona.
- Bischoff, W. (Ed.), 2000. Die Reptilien der Kanarischen Inseln, der Selvagens-Inseln und des Madeira-Archipels. Quelle & Meyer Verlag, Wiebelsheim.
- Bursey, C.R., Goldberg, S.R., 1991. Monthly prevalences of *Physaloptera retusa* in naturally infected Yarrow's Spiny Lizard. J. Wild. Dis. 27, 710–715.
- Bush, A.O., 1990. Helminth communities in avian hosts: determinants of pattern. In: Esch, G., Bush, A.O., Aho, J. (Eds.), Parasite Communities: Patterns and Processes. Chapman & Hall, London, pp. 197–232.
- Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. J. Parasitol. 83, 575–583.
- Carranza, S., 2002. Los métodos moleculares en el estudio de la sistemática y filogenia de los anfibios y reptiles ibéricos. In: Pleguezuelos, J.M., Márquez, R., Lizana, M. (Eds.), Atlas y Libro Rojo de los Anfibios y Reptiles de España (2<sup>a</sup> reimpresión). Dirección General de Conservación de la Naturaleza – Asociación Herpetológica Española, Madrid, pp. 550–579.
- Carretero, M.A., 2004. From set menu to *a la carte*. Linking issues in trophic ecology of Mediterranean lacertids. Ital. J. Zool. 2, 121–133.
- Carretero, M.A., Llorente, G.A., 1991. Alimentación de *Psammmodromus hispanicus* en un arenal costero del nordeste ibérico. Rev. Esp. Herp. 6, 31–44.
- Carretero, M.A., Llorente, G.A., 1993. Feeding of two sympatric lacertids in a sandy coastal area (Ebro Delta, Spain). In: Böhme, W., Pérez-Mellado, V., Valakos, E., Maragou, P. (Eds.), Lacertids of the Mediterranean Region. A Biological Approach. Hellenic Zoological Society, Athens, pp. 155–172.
- Carretero, M.A., Llorente, G.A., Santos, X., Montori, A., 2001. The diet of an introduced population of *Podarcis pityusensis*. Is herbivory fixed? In: Vicente, L., Crespo, E.G. (Eds.), Mediterranean Basin Lacertid Lizards. A Biological Approach. ICN, Lisboa, pp. 113–124.
- Cejudo, D., Márquez, R., Orrit, N., García-Márquez, M., Romero-Bevía, M., Caetano, A., Mateo, J.A., Pérez-Mellado, V., López-Jurado, L.F., 1999. Vulnerabilidad de *Gallotia simonyi* (Sauria, Lacertidae) ante predadores aéreos: influencia del tamaño corporal. Monogr. Herpetol. 4, 149–156.
- Cooper, W.E., Vitt, L.J., 2002. Distribution, extent, and evolution of plant consumption by lizards. J. Zool. 257, 487–517.
- Dearing, M.D., 1993. An alimentary specialization for herbivory in the tropical whiptail lizard *Cnemidophorus murinus*. J. Herpetol. 27, 111–114.



- Escarré, A., Vericad, J.R., 1981. Cuadernos de Fauna Alicantina I. Saurios y Ofidios. Diputación de Alicante, Alicante.
- Font, E., Ferrer, M.J., 1995. *Gallotia galloti* (Canary Islands lizard). Nectar feeding. *Herp. Rev.* 26, 35–36.
- García-Márquez, M., López-Jurado, L.F., Mateo, J.A., 1999a. Características reproductoras y procesos demográficos en una población de *Gallotia caesaris* (Lacertidae) de El Hierro (Islas Canarias). *Monogr. Herpetol.* 4, 223–239.
- García-Márquez, M., Caetano, A., Bello, I., López-Jurado, L.F., Mateo, J.A., 1999b. Ecología del gato cimarrón en el ecosistema termófilo de El Hierro (Islas Canarias) y su impacto sobre el lagarto gigante (*Gallotia simonyi*). *Monogr. Herpetol.* 4, 207–222.
- Harris, D.J., Arnold, E.N., Thomas, R.H., 1998. Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. *Proc. Roy. Soc. London, B* 265, 1939–1948.
- Herrel, A., Vanhooydonck, B., Van Damme, R., 2004. Omnivory in lacertid lizards: adaptive evolution or constraint? *J. Evol. Biol.* 17, 974–984.
- Jover, L., 1989. Nuevas aportaciones a la tipificación trófica poblacional: el caso de *Rana perezi* en el Delta del Ebro. Ph.D. Thesis, University of Barcelona, Barcelona.
- King, G., 1996. Reptiles and Herbivory. Chapman & Hall, London.
- Llorente, G.A., Cejudo, D., Orrit, N., López-Jurado, L.F., 1999. Área propuesta para la reintroducción del lagarto gigante de El Hierro (*Gallotia simonyi*). Análisis de la disponibilidad animal. *Monogr. Herpetol.* 4, 179–195.
- López-Jurado, L.F., 1989. A new Canarian lizard subspecies from El Hierro Island (Canarian archipelago). *Bonn. Zool. Beitr.* 40, 265–272.
- Machado, A., 1985. New data concerning the Hierro Giant lizard and the lizard of Salmor (Canary Islands). *Bonn. Zool. Beitr.* 36, 429–470.
- Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing, Malden.
- Martin, J.E., Roca, V., 2004a. Helminth infracommunities of *Gallotia caesaris caesaris* and *Gallotia caesaris gomerae* (Sauria: Lacertidae) from the Canary Islands (Eastern Atlantic). *J. Parasitol.* 90, 266–270.
- Martin, J.E., Roca, V., 2004b. Helminth infracommunities of a population of the Gran Canaria Giant Lizard *Gallotia stehlini*. *J. Helminthol.* 78, 319–322.
- Martin, J.E., Roca, V., 2005. Helminths of the Atlantic lizard, *Gallotia atlantica* (Reptilia: Lacertidae), in the Canary Islands (Eastern Atlantic): composition and structure of component communities. *Acta Parasitol.* 50, 85–89.
- Martin, J.E., Roca, V., Galdón, M.A., Sánchez-Mut, J., Muniesa, J., 2003. Helminth fauna of *Gallotia caesaris caesaris* (Lehrs, 1914) from El Hierro Island and *Gallotia caesaris gomerae* (Boettger et Müller, 1914) from La Gomera Island (Sauria: Lacertidae). *Rev. Ibér. Parasitol.* 63, 30–35.
- Mateo, J.A., García-Márquez, M., 2002. *Gallotia caesaris*. In: Pleguezuelos, J.M., Márquez, R., Lizana, M. (Eds.), Atlas y Libro Rojo de los Anfibios y Reptiles de España. Dirección General de Conservación de la Naturaleza – Asociación Herpetológica Española, Madrid, pp. 200–201.
- Mateo, J.A., López-Jurado, L.F., García-Márquez, M., 1999. ¿Cuántas especies del género *Gallotia* había en la isla de El Hierro? *Monogr. Herpetol.* 4, 7–16.
- Mautz, W.J., Nagy, K.A., 1987. Ontogenetic changes in diet, field metabolic rate, and water flux in the herbivorous lizard *Dipsosaurus dorsalis*. *Physiol. Zool.* 60, 640–658.
- Orrit, N., Llorente, G.A., López-Jurado, L.F., 1999. Área propuesta para la reintroducción del lagarto gigante de El Hierro (*Gallotia simonyi*). Análisis de la disponibilidad vegetal. *Monogr. Herpetol.* 4, 157–177.
- Pérez-Mellado, V., Corti, C., 1993. Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). *Bonn. Zool. Beitr.* 44, 193–220.
- Pérez-Mellado, V., Romero-Beviá, M., Ortega, F., Martín-García, S., Perera, A., López-Vicente, M., Galache, C., 1999. El uso de los recursos tróficos en *Gallotia simonyi* (Sauria, Lacertidae) de la isla de El Hierro (Islas Canarias). *Monogr. Herpetol.* 4, 63–83.
- Petter, A.J., Quentin, J.C., 1976. Keys to genera of the Oxyuroidea. In: Anderson, R.C., Chabaud, A.G., Willmott, S. (Eds.), CIH Keys to the Nematode Parasites of Vertebrates. CAB International, London, pp. 1–30.
- Pough, F.H., 1973. Lizard energetics and diet. *Ecology* 54, 837–844.
- Rice, W.C., 1989. Analyzing tables of statistical tests. *Evolution* 43, 223–225.
- Roca, V., 1985. Contribución al conocimiento de la helmintofauna de los lacértidos y gekónidos del piso termomediterráneo del Levante ibérico. Unpublished Ph.D. Thesis, Facultad de Ciencias Biológicas, Universidad de Valencia, Valencia.
- Roca, V., 1996. The effect of some factors on the helminth parasite infracommunities of *Podarcis* lizards in the Balearic Islands (Western Mediterranean). *Boll. Soc. Hist. Nat. Bal.* 39, 65–76.
- Roca, V., 1999. Relación entre las faunas endoparásitas de reptiles y su tipo de alimentación. *Rev. Esp. Herp.* 13, 101–121.
- Roca, V., Hornero, M.J., 1991. Diet and helminth fauna in Mediterranean reptiles. *Proc. Medecos VI*, 205–209.
- Roca, V., Hornero, M.J., 1994. Helminth infracommunities of *Podarcis pityusensis* and *Podarcis lilfordi* (Sauria: Lacertidae) from the Balearic Islands (Western Mediterranean Basin). *Can. J. Zool.* 72, 658–664.
- Roca, V., Ferragut, M.V., Hornero, M.J., 1990. Estimaciones corológicas acerca de la helmintofauna de *Lacerta schreiberi* Bedriaga, 1878 (Sauria: Lacertidae) en el Sistema Central (España). *Rev. Esp. Herp.* 4, 93–100.
- Roca, V., Orrit, N., Llorente, G.A., 1999. Parasitofauna del lagarto gigante de El Hierro, *Gallotia simonyi*. *Monogr. Herpetol.* 4, 127–137.
- Roca, V., Carretero, M.A., Llorente, G.A., Montori, A., Martin, J.E., 2005. Helminth communities of two lizard populations (Lacertidae) from Canary Islands (Spain). Host diet–parasite relationships. *Amphibia-Reptilia*, in press.
- Rocha, C.F.D., 1995. Nematode parasites of the Brazilian sand lizard, *Liolaemus lutzae*. *Amphibia-Reptilia* 16, 412–415.

- Sadek, R.A., 1981. The diet of the Madeiran lizard *Lacerta dugesii*. Zool. J. Linn. Soc. 73, 313–341.
- Sanchis, V., Roig, J.M., Carretero, M.A., Roca, V., Llorente, G.A., 2000. Host–parasite relationships of *Zootoca vivipara* (Sauria: Lacertidae) in the Pyrenees (North Spain). Folia Parasitol. 47, 118–122.
- Schluter, D., 1984. Body size, prey size and herbivory in the Galapagos lava lizard, *Tropidurus*. Oikos 43, 291–300.
- Sneath, P.H., Sokal, R.R., 1973. Numerical Taxonomy. Freeman and Co., San Francisco.
- Valido, A., Nogales, M., 2003. Digestive ecology of two omnivorous Canarian lizard species (*Gallotia*, Lacertidae). Amphibia-Reptilia 24, 331–344.
- Van Damme, R., 1999. Evolution of herbivory in lacertid lizards: effects of insularity and body size. J. Herpetol. 33, 663–674.