

Diet and helminth parasites in the Gran Canaria giant lizard, *Gallotia stehlini*

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Abstract: Diet and helminth fauna were analysed in *Gallotia stehlini* (Schenkel, 1901), a giant lacertid lizard endemic to Gran Canaria (Canary Islands, Spain) in order to explore eventual relationships between both traits. This species is mainly herbivorous, eating a large proportion of plant matter (occurrence 97.1%) including not only seeds but also leaves and other vegetative parts. Helminth fauna included many helminth species typical of herbivorous reptiles, and intestinal helminth diversity was high. A comparison with other lacertids suggests that both traits, diet and helminth fauna, result from an adaptation to insular conditions. Canarian *Gallotia*, a separate lineage evolving for a long time in insularity, constitutes the most modified lacertid group in this sense.

Key words: Canary Islands, diet, lizards, parasites.

Resumen: Dieta y helmintos parásitos en el lagarto gigante de Gran Canaria, *Gallotia stehlini*. – Se analizó la dieta y la helmintofauna de *Gallotia stehlini* (Schenkel, 1901), un lagarto gigante endémico de Gran Canaria (Islas Canarias, España), para explorar una eventual relación entre ambos parámetros. Esta especie de lagarto es eminentemente herbívora, con consumo de una alta proporción de materia vegetal (97.1%) que incluyó no sólo semillas sino también hojas y otras partes vegetativas. Su helmintofauna incluyó muchas especies típicas de reptiles herbívoros, y la diversidad de helmintos intestinales fue elevada. La comparación con otros lacértidos sugiere que ambos, dieta y helmintofauna, resultan de una adaptación a condiciones insulares. Los lagartos canarios del género *Gallotia*, un linaje que ha evolucionado durante largo tiempo en condiciones de insularidad, constituyen el grupo de lacértidos más profundamente modificado en este sentido.

Palabras clave: dieta, Islas Canarias, lagartos, parásitos.

INTRODUCTION

Previous studies have reported a relationship between diet (herbivorous vs. carnivorous) and helminth parasites in reptilian hosts (PETTER & QUENTIN, 1976; ROCA, 1999; MARTIN *et al.*, 2005). In particular, herbivorous reptiles are infected by different

Pharyngodonidae than carnivores. In this family of nematodes, PETTER & QUENTIN (1976) recognised two evolutionary lineages (each one of them with different genera) parasitising carnivorous or herbivorous reptiles. Moreover, the structure of helminth communities is richer and more diverse in herbivorous reptiles (ROCA & HORNERO,

1991). It has been suggested (see ROCA, 1999) that the monoxenous life cycle typical of the Pharyngodonidae favours the infection of herbivorous reptile hosts because they have more opportunities to accidentally eat eggs deposited in plants through faecal pellets. Moreover, the increase of plant matter consumed provides a suitable environment for the development of a more rich and abundant helminth fauna (PETTER & QUENTIN, 1976; ROCA, 1999; ROCA *et al.*, 2005). BOUAMER & MORAND (2003) suggested that the evolution of the Pharyngodonidae in the Testudinidae (herbivore hosts) is also related to the habitat selection in the host caecum.

Species or populations of the lizard family Lacertidae living on islands show a higher trend towards herbivory than comparable populations on the mainland (VAN DAMME, 1999) and, when evolutionary history under insular conditions is long enough, true specialisations involving anatomy and behaviour have been demonstrated (CARRETERO *et al.*, 2001; OLESEN & VALIDO, 2003; CARRETERO, 2004; HERREL *et al.*, 2004a). The genus *Gallotia* constitutes an early separated branch of lacertids endemic to the Canary Islands where they arrived soon after the formation of the archipelago (about 23 m.y.a.) and diversified in isolated conditions for more than 12 m.y. (MACA-MEYER *et al.*, 2003). Since all extant members of this genus consume plant matter to some extent (ROCA, 1999), some of the living forms have been used previously for studies of the host diet-parasites relationships (MARTIN *et al.*, 2005; ROCA *et al.*, 2005).

In this study, the diet and helminth parasites of the Gran Canaria giant lizard *Gallotia stehlini* (Schenkel, 1901) have been analysed. This species, naturally distributed only in Gran Canaria island, is one of the four extant "giant" lizards living in the Canary

Islands, together with *G. simonyi* (Steindachner, 1889), *G. bravoana* Hutterer, 1985 and *G. intermedia* Hernández *et al.*, 2000 (MATEO, 2002a, b; MATEO & PÉREZ-MELLADO, 2002; RANDO, 2002; MARTÍN & RANDO, 2006). However, *G. stehlini* is not directly related with the other giant lizards but rather constitutes a branch that separated early in the phylogeny of this genus (MACA-MEYER *et al.*, 2003). A general description of its helminth community has been recently published and its infracommunities and component communities have been analysed (MARTIN & ROCA, 2004a). However, little is known about the diet of this species (BARQUÍN *et al.*, 1986; MOLINA-BORJA, 1986; NARANJO *et al.*, 1991) and thus, the diet-parasite relationships of this lacertid lizard have not been assessed. Nevertheless, the large size of this lizard, insular distribution, herbivory, and the composition and structure of its helminth community make this lizard species useful for such analyses. Hence, the aim of this paper is to investigate the relationship between helminth and diet parameters within *G. stehlini*, 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 sexual variation in diet and parasites, and iv) determination of eventual relationships between helminths and diet. Concerning this last point, we would expect that *G. stehlini*, belonging to an old insular lineage and having a large size, should harbour complex herbivorous helminth faunas (including some helminth species typical of herbivorous reptiles).

MATERIALS & METHODS

Lizard sampling was carried out in Gran Canaria, a volcanic island (1560 km²; 1948 m

maximum elevation) with a central position in the Canary Archipelago, located off the north west coast of Africa, at 27° 44'-28° 10' N and 15° 23'-15° 49' W. The island is microclimatically and ecologically heterogeneous, with strong differences between the north and the south, which has a warmer climate (FERNÁNDEZ-PALACIOS & MARTÍN, 2001). A total of 33 adult *G. stehlini* (13 males, 20 females) were collected by hand in Aldea Blanca (27° 50' N and 15° 28' W, 200 m above sea level), located in the south-eastern part of the island in July 1994 (see MARTÍN & ROCA, 2004a). This locality is considered representative of the typical habitat occupied by this species, which consists of xerophytic areas dominated by volcanic rocks and scattered bushes.

Lizards were transported to the laboratory, sacrificed with an overdose of chloroform and dissected immediately. Snout vent length (SVL) was measured with a digital calliper to the nearest 0.01 mm. No sexual size dimorphism was found in our sample of *Gallotia stehlini* from Gran Canaria (13 males: 121.67 ± 7.33 mm, range 71-161 mm; 20 females: 128.08 ± 4.63 mm, range 96-205 mm; $t_{37} = 0.78$, $p = 0.33$, n.s.). Digestive tracts were removed and 24 stomach contents were suitable for 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 leave and tile pieces in the same way as they do with animal prey instead of chewing them (HERREL *et al.*, 1998). This allowed pooling of both animal and plant matter for analyses. With some exceptions, the order level was used as operational taxonomic unit (OTU; SNEATH & SOKAL, 1973) for identification. Although residence time in the gut may differ between OTUs according to their digestibility (MACKIE, 2002), it is assumed that such bias

would be minimal when comparing, as here, the same digestive compartment between species or classes (CARRETERO & LLORENTE, 2001).

A total of 33 digestive tracts were analysed for helminths under a binocular dissecting microscope. Helminths were counted, washed in saline, fixed, mounted using standard techniques, and identified to species. Unfortunately, due to logistic constraints, information on both diet and parasites could be obtained only from 18 specimens. Although based on a limited data set due to conservation reasons, the results of the present work confirm prior data on other species of *Gallotia* (see Discussion) and are useful for understanding eco-parasitological relationships among Canary lizards.

The descriptors of diet and parasite fauna were: 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 OTUs (CARRETERO *et al.*, 2001; CARRETERO, 2004). The use of descriptive eco-parasitological terms follows BUSH *et al.* (1997).

The following parameters were calculated for both helminth infracommunity and diet for the entire lizard sample as well as separated by sexes: absolute abundance (number of helminths or prey items per lizard), 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 (H_p) was also estimated by the Jack-knife technique (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). All the parameters were calculated as mean individual values and compared by means of ANCOVA. Neither diet nor parasite variables were host size-dependent (see below). However, since such relationships were found in other *Gallotia* species (MARTIN *et al.*, 2005; ROCA *et al.*, 2005), SVL was used as a covariate in the analyses. Furthermore, variables were log-transformed in order to reach normality (assessed by Lilliefors tests). When evaluating simultaneously sets of pair-wise correlations, we did not apply the usual Bonferroni corrections to significance levels because this method greatly inflates the Type II error rate (MORAN, 2003; NAKAGAWA, 2004). Instead, we provide both unadjusted significance values and significance values corrected using the False Discovery Rate procedure (FDS; BENJAMINI & HOCHBERG, 1995).

RESULTS

Diet composition and variation

Table 1 shows the main descriptors of diet for the whole sample and separated by sexes. The diet of adult *G. stehlini* was almost completely herbivorous (97.1% considering seeds and other plant elements). The contribution of the animal matter was much reduced and included nine different taxa, Coleoptera being the most important. There was no sex-related variation in the degree of herbivory or in the consumption of animal items, with the single exception that Formicidae were eaten by females but not by males.

The overall diversity parameters of diet for males, females and males and females pooled are shown in Table 2. None of them correlated with body size ($p > 0.1$). Individual diversity was 8-10 times lower than population diversity in all cases. Females

TABLE 1A, B. Descriptive statistics of diet (Table 1A) and parasite fauna (Table 1B) of *Gallotia stehlini*. N: total number of prey items or parasites (absolute abundance); %P: percentage of occurrence (prevalence); %N: percentage of abundance; IU: resource use index.

TABLE 1A, B. Estadísticos descriptivos de la dieta (Tabla 1A) y la parasitofauna (Tabla 1B) de *Gallotia stehlini*. N: número total de presas o de parásitos (abundancia absoluta); %P: porcentaje de ocurrencia (prevalencia); %N: porcentaje de abundancia; IU: índice de uso del recurso.

TABLE 1A

| | Total | | | | Males | | | | Females | | | |
|--------------------|-------|------|-----|------|-------|------|------|------|---------|------|------|------|
| | N | %P | %N | IU | N | %P | %N | IU | N | %P | %N | IU |
| Seeds | 1036 | 36.4 | 0.2 | 31.5 | 511 | 77.8 | 43.1 | 27.5 | 525 | 80.0 | 30.7 | 29.2 |
| Plant matter | 1744 | 59.9 | 0.4 | 65.5 | 649 | 88.9 | 54.7 | 70.9 | 1095 | 93.3 | 64.1 | 66.6 |
| Coleoptera | 85 | 2.7 | 0.0 | 2.7 | 21 | 55.6 | 1.8 | 1.6 | 64 | 80.0 | 3.8 | 3.8 |
| Orthoptera | 4 | 0.1 | 0.0 | 0.0 | 0 | – | – | – | 4 | 6.7 | 0.2 | 0.0 |
| Hymenoptera | 2 | 0.1 | 0.0 | 0.0 | 1 | 11.1 | 0.1 | 0.0 | 1 | 6.7 | 0.1 | 0.0 |
| Formicidae | 12 | 0.4 | 0.0 | 0.1 | 0 | – | – | – | 12 | 20.0 | 0.7 | 0.3 |
| Diptera | 3 | 0.2 | 0.0 | 0.1 | 1 | 11.1 | 0.1 | 0.0 | 2 | 13.3 | 0.1 | 0.0 |
| Heteroptera | 1 | 0.0 | 0.0 | 0.0 | 1 | 11.1 | 0.1 | 0.0 | 0 | – | – | – |
| Larvae | 4 | 0.1 | 0.0 | 0.1 | 1 | 11.1 | 0.1 | 0.0 | 3 | 20.0 | 0.2 | 0.1 |
| Pupae | 1 | 0.0 | 0.0 | 0.0 | 0 | – | – | – | 1 | 6.7 | 0.1 | 0.0 |
| Arthropoda not id. | 2 | 0.1 | 0.0 | 0.0 | 1 | 11.1 | 0.1 | 0.0 | 1 | 6.7 | 0.1 | 0.0 |

TABLE 1B

| | Total | | | | Males | | | | Females | | | |
|----------------------------------|-------|------|------|------|-------|------|------|------|---------|-------|------|------|
| | N | %P | %N | IU | N | %P | %N | IU | N | %P | %N | IU |
| <i>Thelandros.filiformis.</i> | 6350 | 97.0 | 40.9 | 45.7 | 2635 | 92.3 | 40.8 | 44.8 | 3715 | 100.0 | 41.0 | 46.2 |
| <i>Alaeuris numidica</i> | 4631 | 87.9 | 29.8 | 32.0 | 1825 | 92.3 | 28.2 | 35.7 | 2806 | 85.0 | 31.0 | 29.5 |
| <i>Tachygonetria dentata</i> | 1773 | 60.6 | 11.4 | 9.0 | 477 | 53.9 | 7.4 | 6.4 | 1296 | 65.0 | 14.3 | 9.8 |
| <i>Tachygonetria conica</i> | 1746 | 75.8 | 11.3 | 7.6 | 1047 | 61.5 | 16.2 | 6.7 | 699 | 85.0 | 7.7 | 9.5 |
| <i>Tachygonetria macrolaimus</i> | 28 | 12.1 | 0.2 | 0.1 | 6 | 7.7 | 0.1 | 0.0 | 22 | 15.0 | 0.2 | 0.1 |
| <i>Tachygonetria numidica</i> | 287 | 30.3 | 1.9 | 1.6 | 125 | 23.1 | 1.9 | 1.0 | 162 | 35.0 | 1.8 | 1.6 |
| <i>Parapharyngodon micipsae</i> | 44 | 15.2 | 0.3 | 0.2 | 44 | 38.5 | 0.7 | 0.7 | 0 | 0.0 | 0.0 | 0.0 |
| <i>Parapharyngodon echinatus</i> | 86 | 9.1 | 0.6 | 0.2 | 81 | 15.4 | 1.3 | 0.7 | 5 | 5.0 | 0.1 | 0.0 |
| <i>Parapharyngodon bulbosus</i> | 44 | 9.1 | 0.3 | 0.1 | 25 | 15.4 | 0.4 | 0.1 | 19 | 5.0 | 0.2 | 0.0 |
| <i>Spauligodon atlanticus</i> | 385 | 51.5 | 2.5 | 2.8 | 175 | 46.2 | 2.7 | 3.6 | 210 | 55.0 | 2.3 | 2.3 |
| <i>Skrjabinelazia sp</i> | 144 | 42.4 | 1.0 | 0.7 | 22 | 38.5 | 0.3 | 0.3 | 122 | 45.0 | 1.4 | 1.0 |
| <i>Oochoristica agamae</i> | 2 | 3.0 | 0.0 | 0.0 | 0 | 0.0 | 0.0 | 0.0 | 2 | 5.0 | 0.0 | 0.0 |
| <i>Nematoaenia tarentole</i> | 2 | 3.0 | 0.0 | 0.0 | 0 | 0.0 | 0.0 | 0.0 | 2 | 5.0 | 0.0 | 0.0 |

TABLE 2. Diversity parameters of parasite fauna and diet in *Gallotia stehlini*.TABLA 2. Parámetros de diversidad de la parasitofauna y la dieta en *Gallotia stehlini*.

| | | Total | | Males | | Females | |
|-----------|-----------------|-------|-------------------------|-------|-------------------------|---------|-------------------------|
| | | N | mean ± SEM (range) | N | mean ± SEM (range) | N | mean ± SEM (range) |
| diet | N / lizard | 24 | 125.8 ± 1.5 (0-344) | 9 | 131.8 ± 31.0 (45-344) | 15 | 113.9 ± 30.1 (0-343) |
| | richness | 24 | 3.2 ± 0.3 (0-5) | 9 | 2.8 ± 0.4 (1-5) | 15 | 3.3 ± 0.4 (0-5) |
| | indiv.diversity | 24 | 0.2 ± 0.0 (0-0.5) | 9 | 0.1 ± 0.0 (0-0.4) | 15 | 0.3 ± 0.0 (0-0.5) |
| | pop.diversity | – | 1.2 ± 0.1 (jack-knife) | – | 1.3 ± 0.2 (jack-knife) | – | 1.2 ± 0.1 (jack-knife) |
| | evenness | 24 | 0.4 ± 0.1 (0-0.8) | 9 | 0.3 ± 0.1 (0-0.8) | 15 | 0.5 ± 0.1 (0-0.8) |
| parasites | N / lizard | 33 | 470.4 ± 112.6 (31-2734) | 13 | 497.1 ± 199.3 (31-2734) | 20 | 453.0 ± 137.4 (73-2412) |
| | richness | 33 | 5.0 ± 0.3 (2-7) | 13 | 4.9 ± 0.4 (2-7) | 20 | 5.1 ± 0.4 (2-7) |
| | indiv.diversity | 33 | 0.5 ± 0.0 (0.1-0.1) | 13 | 0.5 ± 0.0 (0.3-0.7) | 20 | 0.5 ± 0.0 (0.1-0.7) |
| | pop.diversity | – | 2.2 ± 0.1 (jack-knife) | – | 2.2 ± 0.2 (jack-knife) | – | 2.1 ± 0.1 (jack-knife) |
| | evenness | 33 | 0.7 ± 0.0 (0.3-0.1) | 13 | 0.8 ± 0.0 (0.4-1.0) | 20 | 0.7 ± 0.0 (0.3-1.0) |

displayed more individual diversity and evenness than males but no significant differences were found for the other parameters (Table 3).

Helminth communities

A total of 13 helminth species were found in the digestive tracts analysed. The intestinal helminth component community of *G.*

stehlini was exclusively composed by nematodes of the families Pharyngodonidae and Seuratidae, all of them living at the end of the intestine (caecum), with the exception of *Skrjabinelazia* sp., which was found in the first part of the intestine. Prevalence and abundance for each helminth species pooled for the whole population and separated by sexes are shown in Table 1. As for the diet,

TABLE 3. ANOVA (and t-test) comparisons for the abundance, richness and diversity of parasite species, and of the diet of lizards.**TABLA 3.** Comparaciones mediante ANOVA (y pruebas de la t) de la abundancia, riqueza y diversidad de las especies parásitas, y de la dieta de los lagartos.

| | | uncorrected | | size-corrected | |
|-----------|-----------------|---------------------------|------|----------------------------|------|
| | | F _{d.f.} | p | F _{d.f.} | p |
| diet | N / lizard | F _{1,22} = 2.00 | 0.17 | F _{1,21} = 1.75 | 0.20 |
| | richness | F _{1,22} = 0.33 | 0.57 | F _{1,21} = 0.26 | 0.61 |
| | indiv.diversity | F _{1,22} = 7.00 | 0.01 | F _{1,21} = 6.56 | 0.02 |
| | pop.diversity | t ₂₂ = 0.32 | 0.76 | — | — |
| | evenness | F _{1,22} = 6.46 | 0.02 | F _{1,21} = 6.03 | 0.02 |
| parasites | N / lizard | F _{1,31} = 0.002 | 0.96 | F _{1,30} < 0.0001 | 0.99 |
| | richness | F _{1,31} = 0.05 | 0.83 | F _{1,30} = 0.08 | 0.79 |
| | indiv.diversity | F _{1,31} = 0.12 | 0.73 | F _{1,30} = 0.10 | 0.75 |
| | pop.diversity | t ₃₁ = 0.57 | 0.29 | — | — |
| | evenness | F _{1,31} = 1.38 | 0.25 | F _{1,30} = 1.35 | 0.25 |

none of the overall diversity parameters of the parasites was correlated with body size ($p > 0.77$). Table 2 shows the diversity parameters of the nematode infracommunities of the hosts. Individual diversity was four times lower than population diversity in all cases.

Host diet-parasite relationships

Helminth fauna and diet were only weakly

associated in *G. stehlini* at the individual level. When considering the whole sample, parasite abundance, richness and diversity correlated with diet evenness but the correlations did not attain significance after FDR correction (Table 4). When the parasite species were considered separately, *Tachygonetria macrolaimus* (Linstow, 1899) was positively correlated with the abundance of plant matter

TABLE 4. Correlation matrix (probability in parentheses) between diet parameters and parasite fauna (N = 18). *Significant when considered isolately. No statistics were significant after applying the FDR procedure.**TABLA 4.** Matriz de correlación (probabilidad entre paréntesis) entre los parámetros de dieta y parasitofauna (N = 18). *Significativos cuando se consideran aisladamente. Los estadísticos no fueron significativos tras la aplicación del procedimiento FDR.

| diet | parasites | | | |
|--------------------|-------------------|-------------------|-------------------|--------------------|
| | N / lizard | richness | diversity | evenness |
| seeds | 0.05 (p = 0.83) | 0.05 (p = 0.82) | -0.15 (p = 0.55) | -0.25 (p = 0.32) |
| other plant matter | 0.41 (p = 0.09) | 0.30 (p = 0.23) | 0.39 (p = 0.11) | 0.24 (p = 0.32) |
| total plant matter | 0.33 (p = 0.17) | 0.26 (p = 0.30) | 0.17 (p = 0.49) | -0.0031 (p = 0.99) |
| abundance | 0.29 (p = 0.25) | -0.01 (p = 0.97) | 0.06 (p = 0.81) | 0.15 (p = 0.54) |
| richness | -0.003 (p = 0.99) | -0.13 (p = 0.60) | -0.19 (p = 0.44) | -0.13 (p = 0.59) |
| diversity | -0.39 (p = 0.11) | -0.38 (p = 0.12) | -0.39 (p = 0.11) | -0.15 (p = 0.56) |
| evenness | -0.49 (p = 0.04)* | -0.46 (p = 0.05)* | -0.46 (p = 0.05)* | -0.17 (p = 0.51) |

without seeds in the stomach, with total plant matter, and with diet abundance (Pearson correlation: $n = 18$, $r = 0.68$, $p = 0.002$; $r = 0.59$, $p = 0.002$, and $r = 0.48$, $p = 0.04$, all but the last significant after FDR correction). Moreover, *Spauligodon atlanticus* was correlated with the abundance of plant matter without seeds ($r = 0.55$, $p = 0.02$). No other significant correlations were found.

DISCUSSION

Diet composition and variation

On the basis of the proportion of plant matter consumed ($> 97\%$), *G. stehlini* can be considered herbivorous in the study area showing a strong trend to folivory. In fact, adaptations for processing leaves have been described in the giant species of *Gallotia* including *G. stehlini*. Such adaptations include specialised dentition (tricuspid teeth), elongated intestines, mechanisms slowing food passage, and intestinal flora capable of digesting cellulose (CARRETERO, 2004; HERREL *et al.*, 2004a). These traits are not found in the smaller, more omnivorous species of the genus, namely *G. galloti*, *G. caesaris* (Lehrs, 1914) and *G. atlantica* Petters et Doria, 1882 (VALIDO & NOGALES, 2003). However, *G. stehlini* is only partially folivorous since a substantial part of its diet still consists of seeds (30-40%), a strategy it shares with the omnivorous species (FONT & FERRER, 1995; COOPER & VITT, 2002). Another Canarian giant lizard, *Gallotia simonyi* (Steindachner, 1889) from El Hierro island, has also been considered basically herbivorous (MACHADO, 1985), although the only evidences of adaptation to herbivory reported for this lizard are a rich fauna of intestinal nematodes (ROCA *et al.*, 1999) and the presence of three cusps per tooth (MATEO *et al.*, 1999). Body size may favour herbivory in lizards, although in Canarian lizards,

CARRETERO (2004) suggested that other factors may be also at play.

Two other main factors linked to insularity (COOPER & VITT, 2002), such as low prey availability and high lizard densities, may be major forces for broadening of the diet to include plants (PÉREZ-MELLADO & CORTI, 1993). In addition, low predation pressure in island ecosystems allows prolonged digestion of plants (VAN DAMME, 1999). BARBADILLO *et al.* (1999) and MATEO (2002b) recorded high densities of *G. stehlini* in Gran Canaria, some populations reaching 1000 individuals/ha. As the Canary Island lizards have no native terrestrial predators, the only potential predators of *G. stehlini* are introduced feral cats, and less likely rats and dogs could predate on these endemic lizards, as is the case with *G. simonyi* from El Hierro island (CEJUDO *et al.*, 1999; GARCÍA-MÁRQUEZ *et al.*, 1999).

Body size is another factor thought to be closely linked to plant consumption by lizards (COOPER & VITT, 2002). Herbivory in lizards is roughly associated with large body size, and this also applies to lacertid lizards (VAN DAMME, 1999). VAN DAMME (1999) concluded that large body size in lacertids is a byproduct of insularity but not a factor directly promoting herbivory. This agrees with the results obtained in the endemic Canarian lizards (*Gallotia* spp.) (MARTIN *et al.*, 2005). In fact, the omnivorous but basically insectivorous *G. atlantica* is smaller than the omnivorous but basically frugivorous *G. galloti* (VALIDO & NOGALES, 2003), while *G. simonyi* and *G. stehlini* are the largest and most herbivorous species.

Recently, VITT (2004) has downplayed the importance of body size as a correlate of herbivory in lizards while giving more importance to thermal ecology. According to this hypothesis, herbivorous lizards, regardless of their size, tend to maintain

higher body temperatures and during longer periods than insectivorous ones in order to digest food with lower profitability. Insular lizards would be able to remain active longer periods without increasing predation risk. Experimental work supports this hypothesis for some lizard groups (ESPINOZA *et al.*, 2004; TRACY *et al.*, 2005; VITT *et al.*, 2005) but not for others (HERREL *et al.*, 2004b). The evidence for *Gallotia* is ambiguous. Further research is needed to disentangle phylogenetic from adaptive influences on thermal ecology of Canarian lizards.

Helminth communities

Although larval forms of helminths have been reported for other Canarian *Gallotia* (MARTIN *et al.*, 2005; MARTIN & ROCA, 2005), none have been found in *G. stehlini*. This suggests that this lizard is not a useful intermediate host for heteroxenous helminth species living in Gran Canaria. In contrast to the situation in *G. stehlini*, four species of cestode larvae were found in the Gran Canaria endemic gekko *Tarentola boettgeri boettgeri* Steindachner, 1891 (ROCA *et al.*, 1999) from the same locality.

The adult cestodes *Oochoristica agamae* Baylis, 1919 and *Nematotaenia tarentolae* López-Neyra, 1944 found in the intestine of one lizard, showed low prevalences and intensities of infection and so they do not take part in the helminth component community of *G. stehlini*. Their presence in *G. stehlini* must be considered as accidental and related to the low consumption of animal matter, with Coleoptera (consumed by this lizard) being the likely useful intermediate hosts for both cestode species.

ROCA *et al.* (1990) suggested that a correlation among host body size and richness and abundance of helminths is common in lizards. However, their samples included both juvenile and adult hosts and

these authors suggested that the reasons for the differences between their helminth communities were related to behavioural differences between juvenile and adult lizards. No correlation was found among body size of *G. stehlini* and parameters of helminth infection and diversity. or between host sex and helminth prevalence, richness or abundance. This agrees with most studies on lacertids (ROCA *et al.*, 1990) which usually do not detect an influence of host sex on the composition and structure of helminth communities of lizards. Nevertheless, minor sexual differences between the helminth communities of male and female *G. caesaris* have been reported from El Hierro (MARTIN *et al.*, 2005). However, there were differences in diet between males and females in this species, whereas this is not the case in *G. stehlini* (see Results).

Host diet-parasite relationships

The intestinal helminth community of *G. stehlini* closely resembles that of *G. caesaris*, in which Pharyngodonidae nematodes are the most common helminths (MARTIN & ROCA, 2004b; MARTIN *et al.*, 2005). Many of these Pharyngodonidae nematodes belong to the evolutionary lineage characteristic of herbivorous reptiles (see introduction and references below) and have never been found in other Palaearctic insular or continental lacertid lizards (ROCA, 1999). In *G. stehlini* these include *Th. fliformis*, *A. numidica*, *T. dentata*, *T. macrolaimus*, *T. conica*, and *T. numidica*. However, helminth abundance and species richness was higher in *G. stehlini* than in *G. caesaris*; in fact, the highest found in a lizard species (MARTIN & ROCA, 2004b). Both facts agree with an important degree of herbivory of *G. stehlini* as shown in its diet analysis (Table 1).

The colonisation of the Canary islands by *Gallotia* is very old (in fact the oldest insular

colonisation among the lacertids, 14-23 m.y.a.; MACA-MEYER *et al.*, 2003). Remarkably, the members of the continental genus *Psammotromus*, sister taxon of *Gallotia* (HARRIS *et al.*, 1998), are almost exclusively arthropodivorous (DÍAZ & CARRASCAL, 1990) and harbour a typically carnivorous helminth fauna (ROCA *et al.*, 1986). This suggests that (partial) herbivory is plesiomorphic in *Gallotia*. However, the phylogeny of *Gallotia* is not completely solved due to a basal tricotomy consisting of a) *G. atlantica*, b) *G. stehlini*, and c) all other species including the other giant lizards and *G. caesaris* (MACA-MEYER *et al.*, 2003). If true, this would imply that herbivory evolved at least twice (in *G. stehlini* and in the other giant lizards) in this genus. Nevertheless, a formal meta-analysis using independent contrasts could be carried out only when a complete ecological and phylogenetic dataset is available.

Moreover, the consumption of plant matter in *Gallotia* is different from that in other, more recent, insular lacertids (i.e. the Balearic and Madeiran species; SADEK, 1981; MARTIN *et al.*, 2005), including not only reproductive organs of the plants but also leaves and stems (VALIDO & NOGALES, 2003). In addition, the following parasitological features are associated with herbivory (ROCA & HORNERO, 1991; ROCA *et al.*, 2005): i) absence of helminth species with indirect life cycles; ii) scarce taxonomic variation at family level, and iii) high values of intensity of infection and of abundance and richness of helminth species.

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