

Fossorial life does not constrain diet selection in the amphisbaenian *Trogonophis wiegmanni*

J. Martín¹, J. Ortega¹, P. López¹, A. Pérez-Cembranos² & V. Pérez-Mellado²

¹ Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain

² Departamento de Biología Animal, Universidad de Salamanca, Salamanca, Spain

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Correspondence

José Martín, Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, 28006 Madrid, Spain. Tel: +34 914111328; Fax: +34 915645078
Email: jose.martin@mncn.csic.es

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Abstract

Morphological adaptations of amphisbaenians for a fossorial life constrain their ecological demands in a greater way than for epigeal reptiles. Studies on the diet of amphisbaenians suggest that most species are generalists, although others seem more selective. However, there is no information on the diet preferences of almost any species because most studies did not evaluate the availability of prey in the environment. We analysed the spring diet selection of a population of the amphisbaenian *Trogonophis wiegmanni* from the Chafarinas Islands, in North Africa. We specifically examined diet estimated from faecal material collected from live amphisbaenians and compared diet with the availability of invertebrates in the soil. Results indicate that the diet of *T. wiegmanni* amphisbaenians consists of some of the types of invertebrates that are more commonly found under rocks used by amphisbaenians, such as insect larvae, snails, isopods, beetles and ants. This diet could be initially considered generalist, and probably opportunistic. However, the comparison of proportions of prey types in the diet and those available in the habitat revealed that *T. wiegmanni* does not eat prey at random, but selects some particular prey types (insect larvae and pupae and, surprisingly, snails), while others (ants and isopods) are consumed less than expected by their abundance. We did not find differences between sexes or age classes in diet composition. We discuss how diet preferences could be due to selection of the more profitable or easily captured prey. There are many aspects of the feeding and foraging biology of amphisbaenians that remain unknown and further studies are clearly needed.

Introduction

Adaptations of amphisbaenians to fossorial life involve important specialized morphological modifications such as the loss of limbs and vision, an elongated body and a compact skull (Gans, 1974, 1978, 2005; Navas *et al.*, 2004). However, these adaptations constrain amphisbaenians to solve their ecological requirements with a suite of original, but often limited, responses different from those of epigeal reptiles (e.g. Papenfuss, 1982; Martín, López & Salvador, 1990, 1991; López, Salvador & Martín, 1998; Colli & Zamboni, 1999; Gomes *et al.*, 2009).

For example, with respect to diet, most amphisbaenian species seem generalists (Cabrera & Merlini, 1990; Cusumano & Powell, 1991; White *et al.*, 1992; Colli & Zamboni, 1999; Kearney, 2003; Bernardo-Silva *et al.*, 2006; Gomes *et al.*, 2009; Balestrin & Cappellari, 2011), although the narrow diets of some species suggest that they could be more selective (López, Martín & Salvador, 1991; Cruz Neto & Abe, 1993; Gil, Guerrero & Pérez-Mellado, 1993; Webb *et al.*, 2000; Vega, 2001; Bernardo-Silva *et al.*, 2006). These studies show

that the diet of amphisbaenians seems mainly limited to the types of small arthropods more often found in the soil, such as ants, termites, adult and larval beetles, or spiders, among others. However, most of these studies did not evaluate the availability of prey in the environment. Thus, there is no information on the diet preferences of almost any amphisbaenian species. Nevertheless, the few studies that have examined availability of prey show that, in the amphisbaenian *Blanus cinereus*, the diet differs from what is available in the soil; amphisbaenians select insect larvae of larger size in higher proportion than their availability, and avoid some of the genera of ants available (López *et al.*, 1991). Also, other amphisbaenians select only a few species of ants from the rich diversity of available species (Esteves, Brandão & Viegas, 2008). These data suggest that, in spite of the restrictions of fossorial life, amphisbaenians can discriminate and select different types of prey. In fact, chemosensory cues may be used by amphisbaenians to identify preferred prey (López & Salvador, 1992, 1994; Semhan, Halloy & Montero, 2010) and to avoid potentially harmful ant species (López & Martín, 1994). To understand the patterns of the diet selection of

amphisbaenians and to evaluate whether these animals prefer and can select some specific prey types or whether they consume prey according to relative abundance, we need more studies that compare the diet of amphisbaenians with the availability of potential prey in their underground habitat.

In this paper, we examine the diet of *Trogonophis wiegmanni* estimated from the faecal material collected from live amphisbaenians, and compare diet with the availability of invertebrates in the soil under rocks similar to those used by amphisbaenians. *Trogonophis wiegmanni* is a representative of the family Trogonophidae in North Africa (Gans, 1960, 2005), where it is found from south-west Morocco to north-east Tunisia (Bons & Geniez, 1996). It lives buried in the soil in areas with sandy soils and leaf litter, and it is usually found under rocks (Civantos, Martín & López, 2003; Martín, López & García, 2013). The ecology of this species is little known, but there are some information on microhabitat use (Civantos *et al.*, 2003; Martín *et al.*, 2013), thermal requirements (Gatten & McClung, 1981; López, Civantos & Martín, 2002), reproductive biology (Bons & Saint Girons, 1963), and social behaviour and population structure (Martín *et al.*, 2011*b,c*). Anecdotal observations indicate that stomach contents of *T. wiegmanni* consist mainly of ants and termites (Bons & Saint Girons, 1963), but precise quantitative information was not provided. In captivity, *T. wiegmanni* feed readily on freshly pre-killed insects, their larvae and pupae being placed under stones (Goetz, 2005).

Material and methods

Study area

We conducted fieldwork at the Chafarinas Islands (Spain), a small archipelago located in the south-western area of the Mediterranean Sea (35°11'N, 2°25'W), 2.5 nautical miles off to the northern Moroccan coast (Ras el Ma, Morocco) and 27 miles to the east of the Spanish city of Melilla. It consists of three small islands: Congreso (25.6 ha), Isabel II (15.1 ha; the only one inhabited) and Rey Francisco (13.9 ha; Martín *et al.*, 2011*a*). The islands present a dry, warm, Mediterranean climate. Vegetation is dominated by plants adapted to the salinity and drought, such as species of the genera *Atriplex*, *Lycium*, *Suaeda* and *Salsola*. The soils are poorly developed and immature (Martín *et al.*, 2013).

Sampling procedures

The study area was visited in March 2012 (spring). We did not sample the area in summer because in this season amphisbaenians are buried deep in the ground and are very hard to find. We haphazardly followed different routes covering all the available habitats on the three islands, during the day between 07:00 and 18:00 (GMT), searching for amphisbaenians by lifting all stones found. Amphisbaenians were abundant and easy to find under stones (Martín *et al.*, 2011*a*). We captured amphisbaenians by hand. Diet samples were obtained by collecting the faeces of live amphisbaenians

in the field. Amphisbaenians usually defecated most gastrointestinal contents when handled, but we also compressed gently their vents to force the expulsion of faeces. Faeces were individually stored in Eppendorf vials. A metallic ruler was employed to measure (to the nearest 1 mm) snout-to-vent length (SVL; from the tip of the snout to the extreme posterior point of the cloacal flap). We considered adults to be those amphisbaenians with an SVL > 120 mm based on maturity of reproductive organs, which correspond to individuals of at least 2.5 years (Bons & Saint Girons, 1963; Martín *et al.*, 2011*c*). We determined sexes of adult amphisbaenians by examining cloacae and carefully everting slightly the hemipenis of males. Juveniles could not be reliably sexed. Amphisbaenians were released at their exact point of capture in less than 5 min after capture. We ensured that the same individuals were not sampled twice by avoiding sampling the same areas twice.

Analyses of faecal contents of amphisbaenians

We analysed the content of faeces under a binocular dissecting microscope. Prey remains were identified according to order or family level always by the same observer (V. P.-M.). Prey numbers for each faecal pellet were estimated conservatively by counting only easily identified remains. Faecal pellet analysis is a standard method to quantify diet without compromising animal well-being (e.g. Martín & Salvador, 1993; Angelici, Luiselli & Rugiero, 1997; Capizzi, 1999; Suarez, Richmond & Case, 2000; Luiselli, 2006; Hawlena & Pérez-Mellado, 2009). Diet reconstruction based on faecal pellet analysis might provide inaccurate estimates of trophic preferences because soft-bodied prey, such as insect larvae and spiders, are destroyed during the digestive process and cannot be identified in faeces (Pincheira-Donoso, 2008). To minimize this possibility, we carefully searched for body parts of small and soft-bodied prey taxa that are less likely to be digested (e.g. head capsules in insect larvae and chelicerae and fragments of cephalic region in spiders). In lizards, diet reconstruction based on such meticulous faecal pellet analysis was found to be highly comparable to diet reconstruction based on gastric contents removed from dissected stomachs, with soft-bodied prey and particularly insect larvae being often equally represented in faecal pellets and gut contents (Pérez-Mellado *et al.*, 2011). Moreover, ethical and conservational reasons argue against the sacrifice of amphisbaenians (Bekoff, 2007).

Availability of invertebrates under rocks

To estimate availability of potential prey in the environment, we walked haphazardly covering the areas and microhabitats where amphisbaenians were found and only during the time of maximum amphisbaenian activity (López *et al.*, 2002; Civantos *et al.*, 2003; Martín *et al.*, 2011*a*, 2013). We randomly lifted stones that might hold amphisbaenians (i.e. we avoided very small stones <10 cm length), and for each stone lifted, we counted for 2 min and identified the invertebrates

(>2 mm long) according to order or family level that were observed on the undersurface of the turned rock and on the substrate exposed on turning, including those that escaped when the rock was lifted, such as isopods, spiders or centipedes (for similar procedures, see Martín & Salvador, 1993; Goldsbrough, Hochuli & Shine, 2003). Simultaneously, we searched for invertebrates, such as insect larvae, buried in the leaf litter or we aimed to record superficial layers of loose dry sandy soil under the rock using a small stick. Thus, invertebrates actually available in the microhabitats and soil layers were used by amphisbaenians (Civantos *et al.*, 2003; J. Martín, pers. obs.). While this estimation method may underestimate the absolute abundance of invertebrates, the standardized record procedure allowed gathering data on the relative abundance of available types of invertebrates comparable to the amphisbaenian diet. This method allows for the recording of fast-moving invertebrates that would escape before we could collect soil samples for counting prey in the laboratory.

Data analyses

Diet composition was described by the relative 'prey presence' (i.e. the percentage of individual amphisbaenians consuming a given prey type) and by the 'prey abundance' (i.e. the percentage of a given prey type relative to the total prey number). The relationship between availability and diet was compared using the Spearman rank correlation. To detect selection for a prey type, we used the selectivity index (D) of Ivlev (1961) modified by Jacobs (1974) according to the formula: $D = (r - p)/(r + p - 2rp)$, where r is the proportion of a given prey type in amphisbaenian diet and P is its proportion available in the environment. Ivlev's selectivity index ranges from -1 (total avoidance) through 0 (no selection) to $+1$ (maximum positive selection). Electivities were tested for significance by using chi-square tests of numbers of each prey type in faeces versus

numbers of all other types in faeces compared to similar habitat data (restricted to groups actually consumed; Sokal & Rohlf, 1995).

Diversity of prey under the rocks and in the diet was calculated by means of the Shannon–Weaver index ($H' = -\sum p_i \ln p_i$) for the taxonomic categories identified (Magurran, 1988). We estimated the food niche breadth (B) of adults and juveniles, and of adult males and females using the inverse of Simpson's diversity index (Pianka, 1973) ($B = 1/\sum p_i^2$), where p_i is the proportional utilization of prey resource i . These indices were standardized by dividing them by the number of used prey categories. To estimate the overlap in diet composition between adults and juveniles, and between males and females, we used the symmetric index of Pianka (1973) [$O_{jk} = (\sum p_{ij}p_{ik}) / \sqrt{(\sum p_{ij}^2)(\sum p_{ik}^2)}$], where p_{ij} is the relative occurrence of taxon i in the diet of age or sex class j and p_{ik} is the relative occurrence of taxon i in the diet of age or sex class k . The index is sealed from 0 to 1 , with 1 indicating complete overlap). We used chi-square tests to compare between age classes or sexes the numbers of each prey type in faeces (Sokal & Rohlf, 1995).

Results

We recorded availability of invertebrates under 118 rocks, of which 111 (94.1 %) contained some invertebrates. Isopods and ants (Formicidae) were the most abundant invertebrates found under the rocks. Snails (Gastropoda), beetles (Coleoptera) and centipedes (Myriapoda) were also important. The invertebrates most frequently found were isopods, snails and beetles, followed by centipedes and ants (Table 1). Other invertebrates such as spiders (Araneae) and silverfish (Thysanura) were also often found under rocks.

We found a total of 120 amphisbaenians, of which 108 (90 %) had some faecal content. Amphisbaenian diet consisted mainly of insect larvae, snails and isopods as the most abundant and frequent prey types (these three types accounting for

Table 1 Total abundance of invertebrates (>2 mm) under rocks at the Chafarinas Islands (North Africa) based on 118 samples. Abundance (total number and %) and mean number (\pm SE) of organisms under each rock are given. Presence refers to the proportion of stones containing a particular organism

	Abundance (n)	Abundance (%)	mean \pm SE	Presence (%)
Gastropoda	167	8.6	1.42 \pm 0.27	39.8
Pseudoscorpiones	6	0.3	0.05 \pm 0.04	2.5
Araneae	30	1.5	0.25 \pm 0.07	18.6
Acarina	10	0.5	0.08 \pm 0.08	0.8
Isopoda	1147	59.1	9.73 \pm 1.87	52.5
Myriapoda	49	2.5	0.42 \pm 0.09	22.9
Thysanura	29	1.5	0.25 \pm 0.07	12.7
Embioptera	16	0.8	0.14 \pm 0.09	4.2
Heteroptera	14	0.7	0.12 \pm 0.08	4.2
Diptera	2	0.1	0.02 \pm 0.01	1.7
Coleoptera	141	7.3	1.49 \pm 0.41	33.9
Formicidae	321	16.5	2.72 \pm 0.91	21.2
Insect larvae	6	0.3	0.05 \pm 0.02	5.1
Lepidoptera pupae	2	0.1	0.02 \pm 0.01	1.7
Total invertebrates	1940		16.44 \pm 2.08	94.1

Table 2 Composition of the diet of *Trogonophis wiegmanni* at the Chafarinas Islands (N. Africa), based on 108 faecal samples collected from live amphisbaenians. Abundance (total number and %) and mean number (\pm SE) of prey in each faecal sample are shown. Presence refers to the percentage of faecal samples containing a particular prey item. The electivity index (D) for each prey type and the statistical significance (P , from a chi-square test) of this index are given

	Abundance (n)	Abundance (%)	mean \pm SE	Presence (%)	Electivity index (D)	P
Gastropoda	33	23.2	0.31 \pm 0.04	30.5	+0.526	<0.0001
Araneae	4	2.8	0.04 \pm 0.02	3.7	+0.311	0.24
Isopoda	15	10.6	0.14 \pm 0.03	13.9	-0.849	<0.0001
Myriapoda	2	1.4	0.02 \pm 0.01	1.8	-0.284	0.41
Heteroptera	5	3.5	0.05 \pm 0.02	4.6	+0.676	0.0002
Coleoptera	13	9.2	0.12 \pm 0.03	11.1	+0.123	0.39
Formicidae	12	8.5	0.11 \pm 0.03	10.2	-0.363	0.012
Insect larvae	47	33.1	0.44 \pm 0.05	43.5	+0.988	<0.0001
Lepidoptera pupae	3	2.1	0.03 \pm 0.02	2.8	+0.911	<0.0001
Arthropoda indeterminate	8	5.6	0.07 \pm 0.03	7.4		
Total invertebrates	142		1.31 \pm 0.06	97.2		

Significant probabilities are marked in bold.

66.9% of the prey), followed by beetles, ants and other insects in lower proportions (Table 2). Some spiders and centipedes were also consumed in low proportions. In addition, we found three faecal samples containing between 50 and 100% of vegetable content. However, because of their low frequency, we considered these vegetable debris as ingested accidentally or coming from the food of some of the amphisbaenians' prey (e.g. larvae), and we did not include them in further analyses.

Overall, there was no significant correlation between the amphisbaenian diet and availability ($r_s = 0.43$, $n = 14$, $t = 1.64$, $P = 0.13$). Diversity of prey under the rocks was lower ($H' = 1.38$) than diversity of prey in the amphisbaenian diet ($H' = 1.73$; excluding unidentified Arthropoda). This was due to the high abundance of isopods under the rocks.

In comparison with the abundance of prey types in the habitat under rocks, amphisbaenians selected positive and significantly insect larvae, butterfly pupae, Heteroptera and snails, and consumed less than expected by their abundance isopods and ants (Table 2). Other types of prey were consumed in similar proportions to their abundance in the habitat.

We found 10 prey type categories in adults and 8 prey types in juveniles. However, the main prey types were similar in both age categories (Table 3). Nevertheless, juveniles seemed to consume lower proportions of snails than adults, but the comparison was not significant ($\chi^2 = 1.18$, $P = 0.28$). Thus, the adjusted food niches for adults ($B = 0.51$) and juveniles ($B = 0.57$) were similar, and there was a high niche overlap ($O = 0.93$).

The diets of adult males and females were similar, with insect larvae and snails being the two main prey types. The adjusted food niches for males ($B = 0.51$) and females ($B = 0.57$) were similar, and there was a high niche overlap ($O = 0.92$) between sexes. However, females consumed a significantly higher proportion of adult beetles than males ($\chi^2 = 4.55$, $P = 0.033$), whereas apparent differences in proportions of snails ($\chi^2 = 0.35$, $P = 0.55$) and isopods ($\chi^2 = 2.52$, $P = 0.11$)

Table 3 Abundance (%) of each prey item in the diet of adult males and females and juveniles *Trogonophis wiegmanni* at the Chafarinas Islands (North Africa)

	Males ($n = 33$)	Females ($n = 45$)	Juveniles ($n = 30$)
Gastropoda	28.9	23.8	14.7
Araneae	0	4.8	2.9
Isopoda	13.3	4.8	17.6
Myriapoda	2.2	0	2.9
Heteroptera	2.2	6.3	0
Coleoptera	2.2	14.3	8.8
Formicidae	8.9	7.9	8.8
Insect larvae	31.1	31.7	38.2
Lepidoptera pupae	2.2	3.2	0
Arthropoda indeterminate	8.9	3.2	5.9
Total prey (n)	45	63	34

were not significant. Also, other prey types were consumed in similar proportions by both sexes ($P > 0.20$ in all cases).

Discussion

The diet of *T. wiegmanni* amphisbaenians consists of some of the types of invertebrates that are more commonly found under rocks used by amphisbaenians, such as insect larvae, snails, isopods, beetles and ants. This diet could be initially considered generalist, and probably opportunistic. However, the comparison of proportions of prey types in the diet to those available in the habitat revealed that *T. wiegmanni* did not eat prey at random, but selected some particular prey types while avoided others. Thus, amphisbaenians preferred insect larvae and pupae and snails, while they consumed less ants and isopods than expected by their abundance. These diet preferences could be due to selection of the more profitable or easily captured prey.

Insect larvae and pupae were positively selected by *T. wiegmanni* probably because larvae provide a high energetic contribution, which would compensate for the cost required for the localization in the subterranean environment. Insect larvae of large size are also positively selected by the amphisbaenian *B. cinereus* (López *et al.*, 1991; Gil *et al.*, 1993), and probably by other amphisbaenians (e.g. Cusumano & Powell, 1991; White *et al.*, 1992; Gomes *et al.*, 2009), although the relationship between diet and availability was not considered in these latter studies. In contrast, other species of amphisbaenians seem to rely more on selecting small but more abundant prey, such as ants and especially termites (Cabrera & Merlini, 1990; Cruz Neto & Abe, 1993; Colli & Zamboni, 1999; Webb *et al.*, 2000; Kearney, 2003; Balestrin & Cappellari, 2011). These differences in the relative contribution of large/scarce versus small/abundant prey might be related to the availability of these prey types in the different habitats, reflecting opportunistic diets, or might result from morphological restrictions for feeding on large prey of the amphisbaenians that possess a more specialized head morphology (Gans, 1968; Webb *et al.*, 2000).

One unexpected result was the inclusion, and positive selection, of a high number of snails in the diet of *T. wiegmanni*. Snails are highly unusual in the diet of other amphisbaenian species and have been only reported as a main prey type in *Amphisbaena ridleyi*, a species endemic to the island of Fernando de Noronha off the coast of Brazil (Pregill, 1984). Molluscs are also reported as a very occasional prey (<0.1%) in *Amphisbaena ibijara* (Gomes *et al.*, 2009). Malacophagy seems to be uncommon in Mediterranean lizards, in spite of the usually high snail abundance in insular ecosystems and their potential profitability (Pérez-Mellado & Corti, 1993). This can be explained by the high costs of handling and crushing their shells (Greene, 1982). Interestingly, *A. ridleyi* has evolved enlarged, molariform dentition (blunt, crushing teeth) (Pregill, 1984), which is similar to those of molluscivorous lizards such as *Varanus niloticus* and *Dracaena guianensis* (Dalrymple, 1979). Gans (1960) described blunt and rounded premaxillary teeth in *T. wiegmanni* and considerably larger and flattened maxillary teeth. Indeed, in contrast to the remaining amphisbaenians, which all possess a pleurodont teeth, trogonophid amphisbaenians have an acrodont dentition and fused maxillary teeth (Gans, 1978), both constituting a possible mechanism to avoid tooth breakage and increase contact with prey items, as it has been interpreted for the molariform dentition in specialized durophagous lizards (Schaerlaeken *et al.*, 2012). Nevertheless, the types of acrodont teeth in other trogonophid amphisbaenians, such as *Diplometopon zarudnyi*, do not seem useful for the crushing of hard-shelled prey (Maisano, Kearney & Rowe, 2006). In addition, the presence of a marked parietal crest in *T. wiegmanni* might allow for the attachment of jaw adductor muscles as it is found in the snail-eating lizard *Chamaeleolis chamaeleonides* (Herrel & Holanova, 2008). Furthermore, the posterior maxillary processes described by Gans (1960) are outward projected, making the skull wider here than at the occipital lobes, offering ample space for an enlarged jaw musculature, as it is inferred from the highly elongated skull (parieto-occipital to

facial ratio, 2 : 1). Alternatively, amphisbaenians might not crush the snail shell but use their teeth to draw the soft body of the snails from their shells as some snakes specialized in feeding on snails do (Hoso, Asami & Hori, 2007). However, similar to what was found in the stomachs of *A. ridleyi*, we found numerous small pieces of crushed shells and of the columella in the faeces of *T. wiegmanni*, which suggest that snails are eaten by crushing. Given its morphology and feeding habits, we suggest that *T. wiegmanni* might be a snail specialist, although further research is needed to confirm this hypothesis.

Some prey types were apparently avoided by amphisbaenians. Ants were consumed in lower proportions than expected by their abundance. This contrasts with other amphisbaenian species where ants and termites are the main prey type (e.g. Riley *et al.*, 1986; Webb *et al.*, 2000; Kearney, 2003). The avoidance of ants in the diet is probably explained because, as it occurs in other amphisbaenians (López *et al.*, 1991; Esteves *et al.*, 2008), only a few species are consumed from those available, leading to a general avoidance of most ants found in the habitat. This may be explained by the difficulty of capturing the most aggressive ant species that can defend themselves very effectively and aggressively against amphisbaenians, especially if they are in groups (López & Martín, 1994). Alternatively, even if amphisbaenians fed on all ant species available, the contagious distribution of ants (i.e. many ants are concentrated in a few ant nests, with many rocks lacking ants) would lead to an apparent avoidance pattern in the diet of amphisbaenians. Also, isopods were consumed in lower proportions than expected. In this case, amphisbaenians may avoid eating this prey as much as expected by their high abundance because isopods have a hard and rigid exoskeleton and amphisbaenians would need a particular and probably not entirely profitable feeding behaviour, which has been observed in captivity (Goetz, 2005; López, Martín & Salvador, 2013). With this feeding behaviour, prey is bitten, the jaws are introduced into the body of the prey to 'scrape' and ingest the body contents until the exoskeleton is completely empty, which may probably increase the nutrient concentration of the prey through removal of low-quality parts (López *et al.*, 2013).

Finally, other prey types, such as beetles, spiders or centipedes, were consumed in proportions similar to their availability, indicating that they were probably consumed when they were found, but that they were not actively selected. Nevertheless, Heteroptera were selected positively, probably because most Heteroptera are soft and easier to ingest than most beetles. Similarly, those invertebrates available but that were not found in the diet of amphisbaenians, such as silverfish or web-spinners, were probably not specifically avoided but would be not represented in the diet because, as they are scarce in the habitat, they were not found in the sample of individual amphisbaenians that we studied.

We have not found any important sex- or age-related differences in diet composition. Sexual dimorphism in head size occurs in *T. wiegmanni*, with males having relatively slightly larger heads than females (Martín *et al.*, 2012). These sexual differences might result in different abilities to feed on differ-

ent prey types, but we found a high niche overlap between sexes, with the only significant difference being that females consumed a higher proportion of adult beetles than males. Sexual differences in diet composition occur in some amphisbaenian species (e.g. Gomes *et al.*, 2009) but not in others (e.g. Balestrin & Cappellari, 2011). Prey size might also vary between sexes, for example, male *B. cinereus* feed on smaller prey than females (Gil *et al.*, 1993). Unfortunately, the fragmentary state of the prey remains in faeces did not allow for obtaining enough reliable measurements of prey size in this study. Similarly, we did not find significant differences in diet composition between adults and juveniles, although juveniles might tend to consume relatively fewer snails than adults, whereas there may be some differences related to maximum prey size (e.g. Gomes *et al.*, 2009). However, because adults still feed on a large amount of small prey types, there would be not so large differences in mean prey size. Also, it has been shown that rather than prey length, prey diameter seems more important, as in several amphisbaenian species prey items vary widely in size but are always smaller in diameter than the gape of the individual that consumed them (Webb *et al.*, 2000; Kearney, 2003).

Still, many aspects of the feeding and foraging biology of this and other amphisbaenians remain unknown, such as the foraging patterns, the methods used to locate, identify and handle prey, and the causes that explain diet variation among species. Given the special ecological and morphological characteristics of amphisbaenians among reptiles, we encourage further studies that should help understand the evolution of many biological and ecological traits.

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