

Soil characteristics determine microhabitat selection of the fossorial amphisbaenian *Trogonophis wiegmanni*

J. Martín¹, P. López¹ & L. V. García²

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

² Departamento de Geoecología, Biogeoquímica y Microbiología Ambiental, Instituto de Recursos Naturales y Agrobiología, CSIC, Sevilla, Spain

Keywords

amphisbaenians; habitat use; *Trogonophis*; soil properties; North Africa.

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

Editor: Mark-Oliver Rödel

Received 13 November 2012; revised 20 February 2013; accepted 20 February 2013

doi:10.1111/jzo.12033

Abstract

Amphisbaenians are reptiles specialized for a fossorial lifestyle, which may limit their opportunities for microhabitat selection in comparison with epigeal reptiles. We hypothesized that, given the fossorial habits of amphisbaenians, a detailed analysis of the physical and chemical properties of the soil may reveal their patterns of habitat use. We investigated microhabitat and soil use by a population of the amphisbaenian *Trogonophis wiegmanni* from the Chafarinas Islands (North-West Africa) and compared them with those available in the habitat. Results showed that some soil physical and chemical characteristics determined microhabitat use by *T. wiegmanni*. Amphisbaenians selected soils that were relatively sandy, basic, carbonated and shallow, having a high cover of medium-sized rocks, whereas they avoided marine salinized, more acid and deeper heavy-textured soils (i.e. with percentages of silt comparatively high), and those covered mainly by small rocks. No differences were found between soils with and without influence of seabird colonies, although this was the main driver of soil chemical variations in these Islands. Vegetation cover *per se* did not seem to have a direct influence on microhabitat use. We discuss how energetic costs of burrowing and the direct and indirect influences of soil chemical properties could explain these patterns of habitat use.

Introduction

Amphisbaenians are reptiles highly specialized for a fossorial lifestyle (i.e. reduced vision, elongated body, compact skull and loss of limbs in most species) (Gans, 1974, 1978, 2005; Navas *et al.*, 2004). These adaptations constrain amphisbaenians to solve their ecological demands with a suite of original responses different from those of epigeal reptiles (e.g. Papenfuss, 1982; Martín, López & Salvador, 1990; Martín, López & Salvador, 1991; López, Salvador & Martín, 1998; Colli & Zamboni, 1999; Webb *et al.*, 2000). However, there is very little information on the ecological requirements of amphisbaenians because of their fossorial secretive habits.

Habitat selection is an important component of the biology of any organism (Huey, 1991). Many surface-living reptiles exploit microhabitats according to their requirements for thermoregulation, foraging, mate searching or predator avoidance (Heatwole, 1977; Huey, 1991). Reptiles can disperse and rely on structural characteristics of the available habitats (vegetation, rocks, etc.) to select an optimal microhabitat (Schoener, 1977). However, in amphisbaenians, morphological modifications, locomotory costs and restrictions for moving through their environment (Gans, 1974; Navas *et al.*, 2004) could decrease their opportunities for microhabitat selection. The amphisbaenian *Trogonophis wiegmanni* uses available types of

vegetation in proportion to their availability, but it avoids areas with small rocks far from bushes (Civantos, Martín & López, 2003). Moreover, soil characteristics directly influence microhabitat selection of the amphisbaenian *Blanus cinereus*, which prefers sandy soils and avoids those with high clay content (Martín *et al.*, 1991). These studies suggest that amphisbaenians do not use habitat randomly. We hypothesized that, given the fossorial habits of amphisbaenians, a more detailed analysis of the physical and chemical characteristics of the soil may further reveal the patterns of habitat selection of these animals. Similarly, soil characteristics may explain the distribution of fossorial skinks (Greenville & Dickman, 2009) and subterranean mammals (Jackson *et al.*, 2008). This is mainly explained by locomotory costs of moving underground, but other factors such as thermoregulation and prey availability may also be important (Martín *et al.*, 1991; Luna & Antinuchi, 2006; Greenville & Dickman, 2009).

The amphisbaenian *T. wiegmanni* is a representative of the family Trogonophidae in North Africa (Gans, 2005), where it is found from southwest Morocco to northeast Tunisia (Bons & Geniez, 1996). It lives buried in the soil and it is usually found under rocks (Civantos *et al.*, 2003). Little research has been carried out on this species, as on other amphisbaenians, but there is some information on its thermal biology (Gatten & McClung, 1981; López, Civantos & Martín, 2002),

reproduction (Bons & Saint Girons, 1963), sexual dimorphism, social behavior and population structure (Martín *et al.*, 2011b,c, 2012). Also, a previous study analyzed some aspects of its habitat use, restricted to vegetation and rock cover (Civantos *et al.*, 2003), but the potential selection of different types of soils has not been considered. We investigated here microhabitat and soil use by *T. wiegmanni*. We specifically studied vegetation and rock cover, and physical and chemical characteristics of the soils available in the habitat, and compared them with those used by amphisbaenians.

Material and methods

Study area

We conducted fieldwork at the Chafarinas Islands (Spain), a small island archipelago located in the south-western area of the Mediterranean Sea (35°11'N, 2°25'W), 2.5 nautical miles to the north of the Moroccan coast (Ras el Ma, Morocco) and 27 miles to the east of the Spanish city of Melilla. It consists of three islands: Congreso (25.6 ha; 137 m asl), Isabel II (15.1 ha; 35 m asl; the only one inhabited) and Rey Francisco (13.9 ha; 31 m asl). Vegetation is conditioned by the arid climate (average annual precipitation of 300 mm), the soil salinity and the guano accumulation from seabird colonies, which induces deep changes in soil chemical properties (García, Marañón & Clemente, 2002a; García *et al.*, 2002b). Plants adapted to the salinity and drought, such as the woody bushes *Salsola oppositifolia*, *Lycium intricatum* and *Atriplex halimus* dominate vegetation. Soils are poorly developed and immature and are characterized by a thin horizon rich in organic matter, which is underlain almost directly by volcanic rocks (andesite or basalt) (Clemente, García & Rodríguez, 1999; García, 2005; García *et al.*, 2007).

Habitat and soil characteristics

We visited the study area for 2 weeks in March 2011. We walked haphazardly covering all the habitats and types of soils available in the three islands (García, 2005). Walks were performed on warm sunny days and between 07:00 and 18:00 (GMT). We lifted all rocks found searching for amphisbaenians, which were fully active under rocks (Martín *et al.*, 2011a). We captured amphisbaenians by hand, measured and released them at their exact point of capture in less than 1 min. Given the high amphisbaenian density (Martín *et al.*, 2011a,c), and because we avoided sampling the same area twice, the probability of repeated sampling of the same individual was very low. We therefore treated all observations as independent.

To characterize microhabitat use of adult amphisbaenians, we took a circular area of 2 m diameter around the rock where the amphisbaenian was found. We estimated visually percent cover of each vegetation type – ‘grasses’ at the ground level, and cover of the three dominant large woody bushes (*Salsola*, *Lycium* and *Atriplex*) above surface level – and

Table 1 Variables (mean \pm SE) that characterize microhabitats and soils available and used by *Trogonophis wiegmanni* amphisbaenians

	Available (n = 39)	Used by <i>T. wiegmanni</i> (n = 40)
Vegetation cover:		
Grasses (%)	24.5 \pm 3.6	24.1 \pm 3.1
<i>Salsola</i> (%)	21.7 \pm 3.2	13.4 \pm 2.6
<i>Lycium</i> (%)	7.2 \pm 2.4	4.1 \pm 1.8
<i>Atriplex</i> (%)	1.7 \pm 1.2	0.6 \pm 0.5
Mean bush height (cm)	65.1 \pm 8.3	73.4 \pm 9.8
Rock cover:		
Small rocks (%)	28.9 \pm 4.4	23.1 \pm 2.8
Medium rocks (%)	9.5 \pm 1.9	35.1 \pm 2.4
Physical characteristics of soil:		
Soil compaction (kg cm ⁻²)	1.8 \pm 0.2	1.5 \pm 0.1
Soil depth (cm)	12.1 \pm 0.9	10.5 \pm 0.8
Gravel (%)	41.2 \pm 2.0	42.3 \pm 1.5
Coarse sand (%)	46.4 \pm 1.6	48.7 \pm 2.4
Fine sand (%)	9.7 \pm 0.5	14.8 \pm 0.7
Silt (%)	15.7 \pm 0.9	18.3 \pm 0.8
Clay (%)	28.1 \pm 0.9	18.1 \pm 1.6
Chemical characteristics of soil:		
pH _{H2O} (1/2.5)	7.58 \pm 0.08	7.95 \pm 0.11
pH _{KCl} (1/2.5)	7.05 \pm 0.09	7.39 \pm 0.09
Total inorganic carbonates (%)	6.0 \pm 0.9	17.3 \pm 1.8
Organic C (%)	3.2 \pm 0.2	3.1 \pm 0.2
N _{Kjeldalh} (%)	0.4 \pm 0.1	0.3 \pm 0.1
P _{Olsen} (mg kg ⁻¹ soil)	294.7 \pm 89.6	180.3 \pm 24.1
Electrical conductivity (dS m ⁻¹)	0.74 \pm 0.12	0.54 \pm 0.05
Na ⁺ _{1/5} (mg kg ⁻¹ soil)	241.4 \pm 22.3	196.2 \pm 16.7
K ⁺ _{1/5} (mg kg ⁻¹ soil)	219.0 \pm 28.2	129.2 \pm 14.2
Ca ⁺⁺ _{1/5} (mg kg ⁻¹ soil)	209.4 \pm 18.7	139.4 \pm 13.9
Mg ⁺⁺ _{1/5} (mg kg ⁻¹ soil)	105.8 \pm 14.9	30.1 \pm 2.1
Cl ⁻ _{1/5} (mg kg ⁻¹ soil)	1069.7 \pm 167.7	387.9 \pm 45.4
NO ₃ ⁻ (mg kg ⁻¹ soil)	36.7 \pm 9.3	24.8 \pm 2.9
NH ₄ ⁺ (mg kg ⁻¹ soil)	133.8 \pm 53.1	48.8 \pm 9.0
SO ₄ ⁻ _{1/5} (mg kg ⁻¹ soil)	98.3 \pm 44.4	148.6 \pm 48.7

calculated ‘mean bush height’ (Table 1). We also estimated percent cover of ‘small rocks’ (6–20 cm) and ‘medium rocks’ (20–60 cm). ‘Soil compaction’ was measured using a hand penetrometer (Eijkelkamp Co., Em Giesbeek, The Netherlands) (Herrick & Jones, 2002). During testing, the penetrometer was pushed vertically into the ground at a slow, steady speed. We measured compaction at five random points close to the central rock and calculated an average value for each site.

Then, we took a bulked soil sample (around 300 g) between the surface and 10 cm depth (or less if the soil was shallower), coinciding with the soil layers used by amphisbaenians (pers. obs.). After taking the soil sample, we excavated until finding the basal rock layer of the soil to determine ‘soil depth’. In the laboratory, soil samples were air-dried, crushed and sieved (<2 mm). Particles between 2 and 60 mm were weighed to calculate the percentage of ‘gravel’ in the sample. Thereafter, we used wet sieving to separate the sand fractions (‘coarse sand’: 2–0.2 mm, and ‘fine sand’: 0.2–0.05 mm). The percent-

age of 'silt' (0.05–0.002 mm) and 'clay' (<0.002 mm) in the fine earth was determined by using the Bouyoucos hydrometer method. We classified 'soil texture classes' based on the relative proportion of the different ranges of sizes of soil particles, following the classification system of the US Department of Agriculture (for details of physical analyses see Dane & Topp, 2002).

We also analyzed chemical characteristics of soil samples. Soil 'total inorganic carbonates' (TIC) were measured using a pressure calcimeter. Organic carbon (C) was determined using a modified Walkley and Black method, and total organic nitrogen (N) using a Kjeldahl digestion and distillation-titration of the produced ammonium. Available phosphorus (P) was extracted using sodium bicarbonate (0.5 M, pH 8.5), and measured by visible spectrophotometry using ammonium molybdate and ascorbic acid. We measured 'pH' with a combined electrode in soil paste with water or KCl (1:2.5). 'Electrical conductivity' was measured electrometrically in aqueous extracts (1:5 soil : water). In these extracts, soluble ions (Na^+ , K^+ , Ca^{2+} , Mg^{2+} , Cl^- , NO_3^- , NH_4^+ and SO_4^{2-}) were measured. Na^+ and K^+ were measured by flame photometry, Ca^{2+} and Mg^{2+} by atomic absorption spectroscopy, Cl^- by titration with AgNO_3 , and NO_3^- , NH_4^+ and SO_4^{2-} by visible spectrophotometry (for details of chemical analyses see Sparks, 1996).

Availability of microhabitats and soils in the study area was estimated along a series of random transects covering the whole area. A sample was taken every 25 m, choosing the nearest stone to a given transect point as the center of the sampling area. Then, we followed the same procedure as when encountering amphisbaenians to measure habitat variables and we took a soil sample for analyses.

Data analyses

We used principal component analysis (PCA) to reduce the 29 microhabitat and soil variables (see Table 1) to a smaller number of independent principal components (PCs). Variables expressed as percentages were subjected to angular transformation; the remainder, except pH, were logarithmically transformed to ensure normality. The initial factorial solutions were rotated by the Varimax procedure to maximize the variance on the new axes and to show a clear pattern of factor loadings (Tabachnick & Fidell, 2007). We used two-way analyses of variance (ANOVAs) to analyze whether the microhabitat and soil characteristics defined by the PC scores differed between sites available and used by amphisbaenians, and among the three islands (Sokal & Rohlf, 1995). We applied a false discovery rate tablewise correction to control for Type I error inflation (Hochberg & Benjamini, 2000; García, 2003, 2004). In addition, we used the meaningful extracted PCs (those with eigenvalues >1) as independent variables in a subsequent discriminant analysis to test whether microhabitat and soil characteristics could be used to predict the presence of amphisbaenians. To detect differences in the use of soil texture classes, we used a χ^2 test and *t*-tests for similarity between percentages.

Results

Average characteristics of microhabitats available and used by *T. wiegmanni* amphisbaenians are described in Table 1. The PCA produced eight PCs with eigenvalues >1 that together accounted for 75.7% of the variance (Table 2). The first PC (PC-1) was a combined salinity-eutrophication soil gradient. It had positive values describing highly eutrophicated (mainly in mineral N and P) and nitrate-enriched-saline ornithogenic soils typical of seagull nesting/roosting areas. PC-1 identified seabird influence as the main driver of soil composition (25% variance explained). The second PC (PC-2) was interpreted as a combined gradient of texture and soil reaction. It described a gradient from basic, sandy soils to heavier (with more silt and clay) and more acidic soils. The third PC (PC-3) described a vegetation gradient from areas with low cover of low bushes (mainly *Salsola*) and with high cover of grasses to areas with high cover of tall *Salsola* bushes. The fourth PC (PC-4) described a gradient of soil shallowness, from areas with deep soils to areas with shallow soils. The fifth PC (PC-5) represented a gradient of soil looseness coupled to a gradient of organic matter enrichment, ranging from compact mineral soils in the negative side to looser soils with high percentages of organic C and N. The sixth PC (PC-6) described a gradient from non-gravelly soils with high cover of *Atriplex* bushes, to soils having high percentages of gravel. The seventh PC (PC-7) described an inverted marine-dependent salinity gradient. It described a gradient from soils enriched in salt of marine origin (i.e. dominated by Na and Cl) with high electrical conductivity to non-saline sandier soils. Finally, the eighth PC (PC-8) represented a combined gradient of stone size and soil TIC content. It ranged from highly carbonated soils with a high cover of medium-sized rocks to soils having a high cover of small rocks and low carbonates content.

There were significant differences between microhabitats available and used by amphisbaenians (Table 3; Fig. 1). The most significant differences were found for PC-8 (rock size-TIC) and PC-7 (marine origin salinity), while PC-2 (texture and soil reaction) and PC-4 (soil depth) were just significant. Thus, according to the relationship of the PCs with the variables (see Table 2), amphisbaenians selected soils relatively sandy, basic, carbonated and shallow, having a high cover of medium-sized rocks, whereas they avoided marine salinized, more acid and deeper heavy-textured soils (i.e. with percentages of silt comparatively high), and those covered mainly by small rocks (Fig. 1). There were also inter-island differences in most PCs (Table 3), which were explained by the different availability of microhabitats and soils in the different islands. The significant interaction terms in PC-2 and PC-8 indicated the different magnitudes of the differences between the characteristics of the microhabitats used by amphisbaenians (which were similar among islands) and the microhabitats available (which differed between islands) (Fig. 1).

The discriminant analysis using the PC scores showed significant differences between available and occupied sites (Wilk's $\lambda = 0.302$, $F_{(8,70)} = 20.52$, $P < 0.0001$). Correct classification was achieved for 95% of the observations of amphisbaenians. Therefore, the presence of amphisbaenians in a

Table 2 Principal components analysis for variables describing microhabitats and soils available and used by *Trogonophis wiegmanni* amphisbaenians

	PC-1	PC-2	PC-3	PC-4	PC-5	PC-6	PC-7	PC-8
Vegetation cover:								
Grasses	-0.07	-0.06	-0.73	-0.23	-0.20	0.05	0.24	0.12
<i>Salsola</i>	-0.01	0.06	0.68	-0.06	0.16	0.24	-0.18	0.15
<i>Lycium</i>	-0.06	0.04	0.03	0.08	0.06	-0.02	0.10	0.09
<i>Atriplex</i>	0.01	0.08	0.05	-0.13	-0.05	-0.80	0.02	0.04
Mean bush height	-0.01	0.12	0.71	-0.06	-0.27	-0.18	0.24	0.05
Rock cover:								
Small rocks	-0.04	-0.03	0.01	0.33	0.03	0.23	0.13	0.64
Medium rocks	0.05	0.04	-0.05	0.25	0.18	0.05	0.22	-0.72
Physical characteristics of soil:								
Soil compaction	0.11	0.38	0.03	-0.08	-0.68	0.23	-0.13	0.06
Soil depth	-0.10	-0.01	-0.05	-0.88	0.03	-0.05	0.10	0.08
Gravel	0.08	0.29	0.28	-0.18	-0.26	0.60	0.19	0.10
Coarse sand	-0.01	-0.95	-0.14	0.04	-0.05	0.02	0.08	-0.15
Fine sand	-0.03	0.17	-0.12	0.25	-0.13	-0.36	0.36	-0.42
Silt	-0.05	0.86	-0.05	0.09	0.06	-0.02	0.04	-0.18
Clay	0.06	0.60	0.27	-0.23	0.10	0.15	-0.31	0.50
Chemical characteristics of soil:								
pH _{H2O}	-0.24	-0.60	0.51	0.01	-0.20	0.22	0.05	-0.17
pH _{KCl}	-0.38	-0.47	0.48	0.04	-0.25	0.31	0.01	-0.14
Total inorganic carbonates	-0.12	-0.44	0.15	0.04	-0.17	0.21	0.06	-0.61
Organic C	0.08	0.16	0.13	-0.06	0.76	0.14	-0.23	-0.08
N	0.34	0.12	0.02	-0.02	0.75	0.06	-0.27	-0.01
P	0.93	-0.03	0.10	0.08	0.21	-0.02	-0.07	0.01
Electrical conductivity	0.73	0.01	-0.02	0.06	0.21	0.03	-0.61	-0.03
Na ⁺	0.17	0.13	0.08	0.01	0.23	-0.01	-0.82	-0.07
K ⁺	0.56	0.18	-0.06	0.02	0.30	-0.22	-0.61	0.06
Ca ⁺⁺	0.69	-0.10	-0.26	-0.02	0.01	0.11	-0.45	0.21
Mg ⁺⁺	0.28	-0.10	-0.01	0.18	-0.11	-0.01	-0.59	0.51
Cl ⁻	0.04	-0.01	0.06	0.03	0.05	-0.01	-0.91	0.23
NO ₃ ⁻	0.89	0.22	0.10	-0.10	0.07	-0.04	-0.14	-0.05
NH ₄ ⁺	0.94	-0.06	0.08	0.08	0.01	-0.08	0.01	0.09
SO ₄ ⁼	0.77	-0.07	-0.24	0.05	-0.01	0.17	-0.02	-0.06
Eigenvalues	7.10	3.33	2.90	2.42	2.14	1.51	1.40	1.16
% Variance explained	24.5	11.5	10.0	8.3	7.4	5.2	4.8	4.0

Correlations in bold lettering correspond to variables sharing at least 30% variance with the components, according to Tabachnick & Fidell (2007).

determined site might be predicted with a high degree of success based on characteristics of the microhabitats and soils defined by the PCs.

With respect to the textural classes of soils, available soils in the islands ranged from the 'loamy sand' to the 'clay' classes, but the most frequent available soils had a 'sandy clay loam' texture. However, amphisbaenians did not significantly use the different types of soils in relationship to their availability ($\chi^2 = 27.30$, 4 d.f., $P < 0.0001$; Fig. 2). Amphisbaenians tended to use more than expected the scarce 'loamy sand' soils (t -test for similarity between percentages, $P = 0.051$) and used significantly more than expected the similarly scarce 'sandy loam' soils (with >60% of sand particles) ($P = 0.0002$), and significantly less than expected the predominant 'sandy clay loam' soils (with >20% of clay particles) ($P < 0.0001$). Amphisbaenians were rarely found in 'clay loam' and 'clay' soils (with >30% of clay particles) ($P > 0.56$ in both cases), but these soils

Table 3 Results (F , P) of two-way analysis of variances testing differences between microhabitats and soils [defined by the different principal component (PC) scores] available and used by *Trogonophis wiegmanni* amphisbaenians in three islands

	Available versus used		Island		Interaction	
	$F_{(1,73)}$	P	$F_{(2,73)}$	P	$F_{(2,73)}$	P
PC-1	0.61	0.44	1.49	0.23	0.38	0.68
PC-2	4.02	0.048	28.79	<0.0001	3.02	0.006
PC-3	0.14	0.71	2.29	0.11	2.14	0.12
PC-4	4.10	0.046	7.08	0.0015	2.09	0.13
PC-5	0.68	0.41	24.59	<0.0001	0.16	0.85
PC-6	0.76	0.39	5.30	0.007	0.22	0.80
PC-7	6.24	0.014	3.26	0.044	2.18	0.12
PC-8	112.05	<0.0001	6.27	0.003	11.23	<0.0001

Significant probabilities after applying a sharpened false discovery rate correction (corrected threshold: $P \leq 0.048$) are marked in bold.

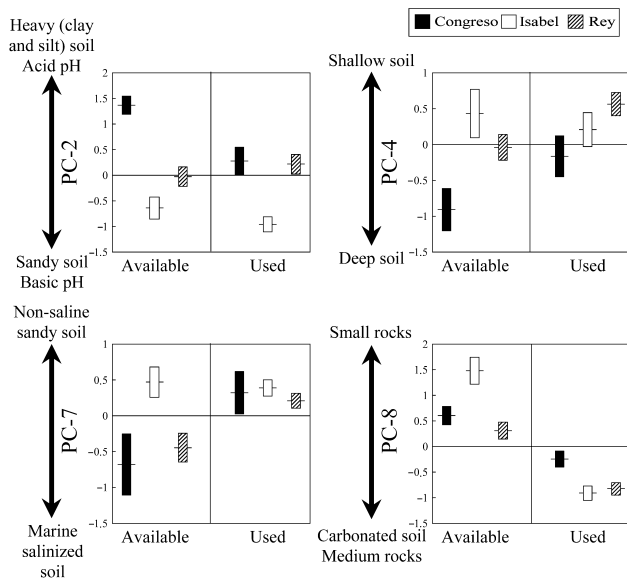


Figure 1 Mean (\pm SE) principal component (PC) scores from a PC analysis on all variables describing microhabitats and soils available and used by *Trogonophis wiegmanni* amphisbaenians in three different islands (solid boxes = Congreso; open boxes = Isabel; dashed boxes = Rey). Only those PC scores differing significantly ($P < 0.05$) between available and used sites are shown.

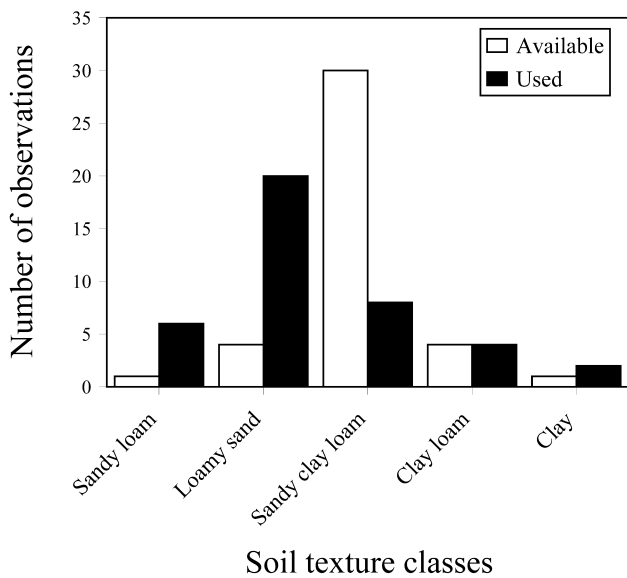


Figure 2 Frequencies of the textural classes of soils available in the habitat (open boxes) and used by *Trogonophis wiegmanni* amphisbaenians (solid boxes).

were also scarce in the islands. In summary, amphisbaenians preferred to use soils of textures coarser than loam and tended to avoid soils of heavier textures, despite the latter being much more frequent.

Discussion

Our study clearly shows that some soil characteristics determined microhabitat use by *T. wiegmanni* amphisbaenians. With respect to the physical characteristics of the soil, amphisbaenians preferred to use loose, sandy, shallow soils, which were available in many parts of the islands, but avoided areas with compact, heavy-textured, deep soils. With respect to the chemical properties of the soil, amphisbaenians preferred basic soils with high percentages of inorganic carbonates and avoided highly saline soils, with lower pH. Finally, amphisbaenians preferred areas with high cover of medium rocks, but avoided areas with high cover of small rocks. In contrast, vegetation cover *per se* did not seem to have a direct influence on microhabitat selection of amphisbaenians (see also Civantos *et al.*, 2003), although correlations between soil properties and vegetation occur (see García *et al.*, 2002a,b).

Several ecological requirements of amphisbaenians could explain these patterns of soil selection. The ability for burrowing and its energetic costs may be a main factor to consider. Thus, soil texture seems to be the main variable that determines habitat selection of amphisbaenians. Sandy loose soils are clearly easier for burrowing, which would reduce costs of foraging, mate searching, etc. Moreover, trogonophid amphisbaenians are especially adapted to dig into sand and have special adaptations to shave sand grains while digging, in contrast to other amphisbaenians that construct tunnels by compacting the soil to the tunnel walls (Gans, 1974). Similarly, soil compaction determines habitat use in other amphisbaenians (Martín *et al.*, 1991), fossorial skinks (Greenville & Dickman, 2009) or subterranean mammals (e.g. Hansson, 1982; Jackson *et al.*, 2008). In subterranean rodents, energetic costs of movement underground increase considerably in hard soil types (Luna & Antinuchi, 2006). Energetic costs of sand swimming in the golden mole are less than one-tenth of the energy required by rodents tunneling through compact soils (Seymour, Withers & Weathers, 1998). In addition, soil compaction and soil porosity can restrict the mobility and activity of soil invertebrates (Whalley, Dumitru & Dexter, 1995), leading to low abundances of potential prey for amphisbaenians. On the other hand, soil texture has a strong influence on soil water retention and availability. In arid areas, fine textured ('heavy') soils hold scarcer amount of the rainwater they receive at lower matrix potentials than coarse-textured soils at the same water content (the 'inverse texture effect', Noy-Meir, 1973). Furthermore, the higher saturated hydraulic conductivity allows coarser soils to infiltrate a higher proportion of rainfall water (Fernández-Illescas *et al.*, 2001). Therefore, under arid or semiarid conditions, fossorial organisms are subjected to higher water losses in heavier than in coarser soils.

Some chemical characteristics of the soil also influenced microhabitat selection of *T. wiegmanni*. Contrary to what we expected, the main soil chemical gradient, related to seabird products accumulation, did not contribute to explain habitat selection. However, amphisbaenians avoided saline soils enriched in salt of marine origin (i.e. dominated by Na and Cl) with high electrical conductivity. In fact, there are

conspicuous gaps in the microgeographic distribution of *T. wiegmanni* in Congreso island (Martín *et al.*, 2011a), which coincide with the distribution of highly to extremely saline soils (Clemente *et al.*, 1999; García, 2005). Soil water osmotic potential is inversely related to soil salinity (Bresler, McNeal & Carter, 1982). This implies that soil water availability is much lower for organisms living in saline soils, which should affect directly osmoregulation of amphisbaenians (Shoemaker & Nagy, 1977). Extremely high salinity may cause osmotic dehydration of animal tissues and intoxication by the excess of some soluble ions (e.g. Na, Cl). Also, salinity imposes a strong physiological filter, with only a small number of species being able to cope with high salinity levels, which reduces the abundance and diversity of vegetation and potential prey of amphisbaenians (García *et al.*, 1993; McKenzie, Burbidge & Rolfe, 2003).

Also, *T. wiegmanni* amphisbaenians preferred soils with a more basic pH, even when soil textures were similar, and with high concentrations of inorganic carbonates. The reasons of such patterns are not clear, but they might be related to the abundance of invertebrate macrofauna that are potential prey of amphisbaenians, which is intimately linked to chemical and physical attributes of the soil. On the one hand, soil acidity reduces the diversity and abundance of macrofauna and mesofauna and the activity of decomposer organisms (e.g. Geissen, Gehrman & Gensler, 2007; Moço *et al.*, 2010). Therefore, the selection of basic soils might also be partly related to high abundances of prey. Alternatively, because total salinity and pH are negatively correlated in calcareous soils (Al-Busaidi & Cookson, 2003), amphisbaenians might simply use more basic soils because they avoid saline soils.

Inorganic carbonates were more abundant in the sites used by *T. wiegmanni*. One possible reason for this is that carbonates came partly from the rests of shells of the very abundant terrestrial snails that take refuge under rocks (pers. obs.). Snails are an important prey of *T. wiegmanni* (unpubl. data), and their abundance might explain the use of these sites by amphisbaenians. Abundance of carbonates also contributes to buffer soil pH in the basic range (around 8). An interesting indirect effect of seagull colonies on amphisbaenians distribution may be related to the remotion of the soil inorganic carbonate reserve (followed by a decrease of soil pH) caused by the acid products derived from bird feces and their subsequent mineralization (see García *et al.*, 2002b; García, 2008).

Rock cover was also important in microhabitat selection of *T. wiegmanni*, as it was found previously (Civantos *et al.*, 2003). Rocks of an appropriate medium-size are used for amphisbaenians to thermoregulate under them without being exposed to predators (Martín *et al.*, 1990; López *et al.*, 1998, 2002). Rock size is important because the thermal environment deviates from the range of selected temperatures significantly less under rocks selected by *T. wiegmanni* than it does beneath available rocks (López *et al.*, 2002). Relative humidity is also higher beneath stones, which is important in this arid environment. Also, many social interactions occur under rocks (Martín *et al.*, 2011b). Finally, a high diversity of potential prey are found sheltering under rocks but not buried in the soil (López, Martín & Salvador, 1991).

We conclude that physical and chemical properties of the soil significantly influence microhabitat use of *T. wiegmanni* amphisbaenians. Different amphisbaenian species have evolved diverse adaptations for burrowing, especially in head size and shape, and in excavation patterns (Gans, 1974; Navas *et al.*, 2004). Thus, some amphisbaenian species have a higher ability than others for digging in hard substrates (Gans, 1974). Future studies should consider soil selection patterns of several species of amphisbaenians to analyze a possible relationship between selected soil types and burrowing ability. The influence of soil chemical properties on invertebrate prey should also be examined.

Acknowledgments

We thank two anonymous reviewers for their helpful comments. The field station of the 'Refugio Nacional de Caza de las Islas Chafarinas' provided logistical support. Transport was provided by the Ministerio de Medio Ambiente's boat 'Zafarín' and evacuation from the islands by a Super Puma helicopter from the Spanish Army. We thank Javier Díaz and Gonzalo Martínez for friendship and help in the Islands and Eduardo Gutiérrez for helping with laboratory analyses. Legal authorization and financial support was provided by the 'Organismo Autónomo de Parques Nacionales', with additional financial support from a Ministerio de Ciencia e Innovación project (CGL2011-24150/BOS) and from a Regional Government of Andalusia project (P09-RNM-4987).

References

- Al-Busaidi, A.S. & Cookson, P. (2003). Salinity–pH relationships in calcareous soils. *J. Agric. Mar. Sci.* **8**, 41–46.
- Bons, J. & Geniez, P. (1996). *Amphibians and reptiles of morocco*. Barcelona: Asociación Herpetológica Española.
- Bons, J. & Saint Girons, H. (1963). Ecologie et cycle sexuel des amphisbeniens du Maroc. *Bull. Soc. Sci. Nat. Phys. Maroc.* **43**, 117–158.
- Bresler, E., McNeal, B.L. & Carter, D.L. (Eds) (1982). *Saline and sodic soils: principles-dynamics-modelling*. New York: Springer-Verlag.
- Civantos, E., Martín, J. & López, P. (2003). Fossorial life constrains microhabitat selection of the amphisbaenian *Trogonophis wiegmanni*. *Can. J. Zool.* **81**, 1839–1844.
- Clemente, L., García, L.V. & Rodríguez, A. (1999). Los suelos de la Isla del Congreso (Chafarinas). In *Avances en el estudio del Cuaternario español*: 201–206. Pallí-Buxó, L. & Roque-Pau, C. (Eds). Gerona: Actas de la X Reunión Nacional de Cuaternario.
- Colli, G.R. & Zamboni, D.S. (1999). Ecology of the worm-lizard *Amphisbaena alba* in the Cerrado of Central Brazil. *Copeia* **1999**, 733–742.
- Dane, J.H. & Topp, G.C. (Eds) (2002). *Methods of soil analysis. Part 4. Physical methods*. Madison: Soil Science Society of America and American Society of Agronomy.

- Fernández-Illescas, C.P., Porporato, A., Laio, F. & Rodríguez-Iturbe, I. (2001). The ecohydrological role of soil texture in water-limited ecosystems. *Water Resour. Res.* **37**, 2863–2872.
- Gans, C. (1974). *Biomechanics: an approach to vertebrate biology*. Philadelphia: Lippincot.
- Gans, C. (1978). The characteristics and affinities of the Amphisbaenia. *Trans. Zool. Soc. Lond.* **34**, 347–416.
- Gans, C. (2005). Checklist and bibliography of the amphisbaenia of the world. *Bull. Am. Mus. Nat. Hist.* **280**, 1–130.
- García, L.V. (2003). Controlling the false discovery rate in ecological research. *Trends Ecol. Evol.* **8**, 553–554.
- García, L.V. (2004). Escaping the Bonferroni iron claw in ecological studies. *Oikos* **105**, 657–663.
- García, L.V. (2005). Suelos de las Islas Chafarinas y sus relaciones ecológicas. *Ecosistemas* **14**, 135–139.
- García, L.V. (2008). Isótopos estables como trazadores de la influencia aviaria en suelos y plantas. In *Técnicas y aplicaciones multidisciplinarias de los isótopos ambientales*: 305–323. Alcorlo, P., Redondo, E. & Toledo, J. (Eds). Madrid: Universidad Autónoma de Madrid.
- García, L.V., Clemente, L., Gutiérrez, E. & Jordán, A. (2007). Factores condicionantes de la diversidad edáfica en las islas Chafarinas. In *Tendencias actuales de la ciencia del suelo*: 828–833. Bellinfante, N. & Jordán, A. (Eds). Sevilla: Universidad de Sevilla.
- García, L.V., Marañón, T. & Clemente, L. (2002a). Animal influences on soil properties and plant cover in the Chafarinas Islands (NW Africa). In *Man and soil at the third millennium* Vol. 1: 705–712. Rubio, J.L., Morgan, R.P.C. & Asins, S. (Eds). Logroño: Geoforma.
- García, L.V., Marañón, T., Moreno, A. & Clemente, L. (1993). Aboveground biomass and species richness in a Mediterranean salt marsh. *J. Veg. Sci.* **4**, 417–424.
- García, L.V., Marañón, T., Ojeda, F., Clemente, L. & Redondo, R. (2002b). Seagull influence on soil properties, chenopod shrub distribution, and leaf nutrient status in semi-arid Mediterranean islands. *Oikos* **98**, 75–86.
- Gatten, R.E. & McClung, R.M. (1981). Thermal selection by an amphisbaenian, *Trogonophis wiegmanni*. *J. Therm. Biol.* **6**, 49–51.
- Geissen, V., Gehrman, J. & Gensler, L. (2007). Relationships between soil properties and feeding activity of soil fauna in acid forest soils. *J. Plant Nutr. Soil Sci.* **170**, 632–639.
- Greenville, A.C. & Dickman, C.R. (2009). Factors affecting habitat selection in a specialist fossorial skink. *Biol. J. Linn. Soc.* **97**, 531–544.
- Hansson, L. (1982). Experiments on habitat selection in voles: implications for the inverse distribution of two common European species. *Oecologia* **52**, 246–252.
- Heatwole, H. (1977). Habitat selection in reptiles. In *Biology of the Reptilia, vol. 7. Ecology and behavior A*: 137–155. Gans, C. & Tinkle, D.W. (Eds). New York: Academic Press.
- Herrick, J.E. & Jones, T.L. (2002). A dynamic cone penetrometer for measuring soil penetration resistance. *Soil Sci. Soc. Am. J.* **66**, 1320–1324.
- Hochberg, Y. & Benjamini, Y. (2000). On the adaptive control of the false discovery rate in multiple testing with independent statistics. *J. Educ. Behav. Stat.* **25**, 60–83.
- Huey, R.B. (1991). Physiological consequences of habitat selection. *Am. Nat.* **137**, 95–115.
- Jackson, C.R., Lubbe, N.R., Robertson, M.P., Setsaas, T.H., van der Waals, J. & Bennett, N.C. (2008). Soil properties and the distribution of the endangered Juliana's golden mole. *J. Zool. (Lond.)* **274**, 13–17.
- López, P., Civantos, E. & Martín, J. (2002). Body temperature regulation in the amphisbaenian *Trogonophis wiegmanni*. *Can. J. Zool.* **80**, 42–47.
- López, P., Martín, J. & Salvador, A. (1991). Diet selection by the amphisbaenian *Blanus cinereus*. *Herpetologica* **47**, 210–218.
- López, P., Salvador, A. & Martín, J. (1998). Soil temperatures, rock selection and the thermal ecology of the amphisbaenian reptile *Blanus cinereus*. *Can. J. Zool.* **76**, 673–679.
- Luna, F. & Antinuchi, C.D. (2006). Cost of foraging in the subterranean rodent *Ctenomys talarum*: effect of soil hardness. *Can. J. Zool.* **84**, 661–667.
- Martín, J., López, P. & Salvador, A. (1990). Field body temperatures of the amphisbaenid lizard *Blanus cinereus*. *Amphib-Reptil.* **11**, 87–96.
- Martín, J., López, P. & Salvador, A. (1991). Microhabitat selection of the amphisbaenian *Blanus cinereus*. *Copeia* **1991**, 1142–1146.
- Martín, J., Polo-Cavia, N., Gonzalo, A., López, P. & Civantos, E. (2011a). Distribución, abundancia y conservación de la culebrilla mora (*Trogonophis wiegmanni*) en las Islas Chafarinas. *Bol. Asoc. Herp. Esp.* **22**, 107–112.
- Martín, J., Polo-Cavia, N., Gonzalo, A., López, P. & Civantos, E. (2011b). Social aggregation behaviour in the North African amphisbaenian *Trogonophis wiegmanni*. *Afr. J. Herpetol.* **60**, 171–176.
- Martín, J., Polo-Cavia, N., Gonzalo, A., López, P. & Civantos, E. (2011c). Structure of a population of the amphisbaenian *Trogonophis wiegmanni* in North Africa. *Herpetologica* **67**, 250–257.
- Martín, J., Polo-Cavia, N., Gonzalo, A., López, P. & Civantos, E. (2012). Sexual dimorphism in the North African amphisbaenian *Trogonophis wiegmanni*. *J. Herpetol.* **46**, 338–341.
- McKenzie, N.L., Burbidge, A.H. & Rolfe, J.K. (2003). Effect of salinity on small, ground-dwelling animals in the Western Australian wheatbelt. *Aust. J. Bot.* **51**, 725–740.
- Moço, M.K.S., Gama-Rodrigues, E.F., Gama-Rodrigues, A.C., Machado, R.C.R. & Baligar, V.C. (2010). Relationships between invertebrate communities, litter quality and soil attributes under different cacao agroforestry systems in the south of Bahia, Brazil. *Appl. Soil Ecol.* **46**, 347–354.

- Navas, C.A., Antoniazzi, M.M., Carvalho, J.E., Chaui-Berlink, J.G., James, R.S., Jared, C., Kohlsdorf, T., Pais-Silva, M.D. & Wilson, R.S. (2004). Morphological and physiological specialization for digging in amphisbaenians, an ancient lineage of fossorial vertebrates. *J. Exp. Biol.* **207**, 2433–2441.
- Noy-Meir, I. (1973). Desert ecosystems: environment and producers. *Annu. Rev. Ecol. Syst.* **4**, 25–44.
- Papenfuss, T.J. (1982). The ecology and systematics of the amphisbaenian genus *Bipes*. *Occ. Pap. Calif. Acad. Sci.* **136**, 1–42.
- Schoener, T.W. (1977). Competition and the niche. In *Biology of the reptilia, vol. 7, ecology and behavior A*: 35–136. Gans, C. & Tinkle, D.W. (Eds). New York: Academic Press.
- Seymour, R.S., Withers, P.C. & Weathers, W.W. (1998). Energetics of burrowing, running, and free-living in the Namib desert golden mole (*Eremitalpa namibensis*). *J. Zool. (Lond.)* **244**, 107–117.
- Shoemaker, V.H. & Nagy, K.A. (1977). Osmoregulation in amphibians and reptiles. *Annu. Rev. Physiol.* **39**, 449–471.
- Sokal, R.R. & Rohlf, F.J. (1995). *Biometry*. 3rd edn. New York: W.H. Freeman and Co.
- Sparks, D.L. (Ed.) (1996). *Methods of soil analysis. Part 3. Chemical methods*. Madison: Soil Science Society of America and American Society of Agronomy.
- Tabachnick, B.G. & Fidell, L.S. (2007). *Using multivariate statistics*. 5th edn. London: Pearson Education Inc.
- Webb, J.K., Shine, R., Branch, W.R. & Harlow, P.S. (2000). Life underground: food habits and reproductive biology of two amphisbaenian species from South Africa. *J. Herpetol.* **34**, 510–516.
- Whalley, W.R., Dumitru, E. & Dexter, A.R. (1995). Biological effects of soil compaction. *Soil Tillage Res.* **35**, 53–68.