

Fossorial life constrains microhabitat selection of the amphisbaenian *Trogonophis wiegmanni*

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Abstract: We present a field study designed to characterize microhabitat selection in a population of *Trogonophis wiegmanni*, a fossorial reptile that is the only representative of the family Trogonophidae in North Africa. Our results show that *T. wiegmanni* used microhabitats in proportion to their availability with one exception: they showed a preference for areas with 5–10 cm high vegetation cover (i.e., perennial bushes and scrubs such as *Atriplex halimus*, *Lycium intricatum*, and *Suaeda vera*, and herbs such as *Lavatera mauritanica* and *Malva parviflora*). They avoided areas with abundant small stones, indicating that at least some structural characteristics of the microhabitat occupied by amphisbaenians seem to be different from those available. Our data also show that *T. wiegmanni* selected thinner and wider rocks than those rocks found randomly. Such choices could have important thermoregulatory consequences.

Résumé : Notre étude de terrain cherche à caractériser la sélection de l'habitat chez une population de *Trogonophis wiegmanni*, un reptile fouisseur, seul représentant de la famille des Trogonophidae en Afrique du Nord. *Trogonophis wiegmanni* utilise les microhabitats en proportion de leur disponibilité, mais à une exception près : il montre une préférence pour les milieux qui possèdent un couvert végétal de 5–10 cm de hauteur (i.e., des arbustes permanents et des broussailles, tels que *Atriplex halimus*, *Lycium intricatum* et *Suaeda vera*, et des plantes herbacées, telles que *Lavatera mauritanica* et *Malva parviflora*). Il évite les endroits couverts de pierraille, ce qui indique que certaines caractéristiques des microhabitats occupés par les amphisbaniens semblent différer de ce qui est généralement disponible en nature. Nos données indiquent aussi que *T. wiegmanni* choisit des pierres plus minces et plus larges que les pierres disponibles au hasard. Ces choix ont peut-être d'importantes conséquences sur la thermorégulation.

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Introduction

Habitat selection is an important feature of behavior and population dynamics and has therefore received much attention (Bell et al. 1994). Among factors affecting habitat selection, habitat quality is one of the most important (Schoener and Schoener 1982; Huey 1991). The evaluation of habitat quality is a central topic in contemporary ecological studies and requires the integration of a large number of synergistic factors (e.g., limitation by physical constraints, predation risk, mating opportunities, resource availability; Huey 1991). A high-quality habitat may be defined by its greater microhabitat diversity or the prevalence of favorable microhabitat characteristics (Fox 1983) and by enhanced complexity of vegetational cover (Civantos 2000).

Many reptiles rely primarily on structural characteristics of their environment in habitat selection (Schoener 1977). Numerous autoecological studies have indicated characteristic features of habitats selected by particular species (Heatwole 1977). Selective exploitation of microhabitats allows many reptiles to maintain body temperatures within a

range that optimizes physiological capacities and ultimately ecological performance (Huey 1991). Many surface-dwelling reptiles exploit available microhabitats according to their requirements for thermoregulation (Scheibe 1987; Paulissen 1988), foraging (Henderson 1974; Paulissen 1988), or predator avoidance (Stamps 1983). Some microhabitats may supply better refuges against predators or provide more or higher quality food (Martín and Salvador 1992; Martín and López 1998), and thus microhabitat use may influence survival (Tracy 1982; Civantos 2000).

Amphisbaenians are adapted to burrowing life; vision is reduced, and hearing and olfactory capabilities are enhanced. These adaptations constrain amphisbaenians to solve their ecological demands with a suite of original responses different from those of other epigeal reptiles (e.g., Papenfuss 1982; Martín et al. 1990, 1991; López et al. 1991, 1998). These modifications and their locomotory restrictions could also influence their possibilities for habitat selection (Gans 1978). However, only one study has examined whether amphisbaenians select some optimal microhabitats or whether they are constrained to use all available microhabitats (Martín et al. 1991). More studies are necessary to know how these special adaptations to fossorial life influence microhabitat use of the different amphisbaenian species in different ecological contexts.

We studied the microhabitat use of a population of the amphisbaenian *Trogonophis wiegmanni*, a fossorial reptile that is the only representative of the family Trogonophidae in North Africa (Bons and Geniez 1996). It is a Mograbin endemic with a range in the Mediterranean biome, from

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southwest Morocco to northeast Tunisia. Its elongate limbless body, reduced vision, and compact skull are morphological adaptations for burrowing (Gans 1974, 1978). Thus, it lives buried in sandy soils or abundant leaf litter and frequently uses stones for thermoregulation and foraging. Amphisbaenians are typical thigmotherms that obtain heat through contact with the soil and stones. This suggests that amphisbaenians occupy rocks with thermal properties suitable to maintain their preferred body temperature. Amphisbaenians seem able to maintain their preferred temperatures by moving vertically between cooler areas deep below the surface and warmer areas nearer the surface and by actively selecting rocks of different thickness at different times of day (López et al. 1998, 2002). Therefore, amphisbaenians are usually found under rocks or dead wood, especially in the wetter seasons, whereas they are usually buried in the ground in the dry summer (Bons and Geniez 1996). This species has been scarcely studied, but there are some data on their thermoregulatory behavior (Gatten and McClung 1981; López et al. 2002), aerobic and anaerobic activity metabolism (Kamel and Gatten 1983), and reproductive cycle (Bons and Saint Girons 1963). However, to our knowledge this is the first study regarding microhabitat selection of this species. The purpose of this study was to characterize microhabitat selection in a population of *T. wiegmanni* inhabiting a dry environment in northern Africa by comparing habitat factors associated with *T. wiegmanni* found under stones and a set of locations chosen at random from the general habitat. We also tested for differences in microhabitat selection between age classes and the sexes.

Materials and methods

We conducted the fieldwork at the Chafarinas Islands (Spain). The archipelago of the Chafarinas is located in the southwestern area of the Mediterranean sea (35°11'00"N, 2°25'35"W), 2.5 naut. mi. (1 naut. mi. = 1.852 km) to the north of the Moroccan coast (Ras el Ma, Morocco) and 43.4 km to the east of the Spanish city of Melilla. It consists of three islands named Congreso, Isabel II (the only inhabited island), and Rey Francisco. Congreso is the westernmost, largest (25.6 ha), and highest island (137 m asl). Isabel II (15.1 ha, 35 m asl), located between Congreso (at 1 km) and Rey Francisco (at 175 m), is the easternmost, smallest (13.9 ha), and lowest (31 m asl) island of the three. The islands present a Mediterranean dry and warm climate strongly influenced by the dominant winds from east to west. The vegetation is conditioned by the aridity of the climate (average annual precipitation 300 mm), high salinity, and guano accumulation from numerous seabirds colonies. The current vegetation is dominated by plants adapted to salinity and drought, including *Atriplex halimus*, *Salsola oppositifolia*, *Suaeda vera*, and *Lycium intricatum* bushes. In general, the soils of the islands are little developed and immature, and are characterized by a thin layer rich in organic matter where the vegetation settles, followed almost directly by the volcanic original rock (andesite or basalt).

The area was visited regularly during March and occasionally from May to June 2000. We haphazardly walked 73 different random routes (approximately 100 m/h) covering all the habitats available on the islands. The transects were

walked at specific times for a total of 19 days in March and 11 days in May–June between 0700 and 1800 (GMT), searching for amphisbaenians by lifting all stones that were found. Amphisbaenians were typically found active under stones. When an amphisbaenian was found under a stone, we quantified the microhabitat structure associated with that stone. We took four 4-m transects, one at each of the four cardinal orientations radiating from the stone. Using a scored stick held vertically, we recorded the number of contacts with the stick of grass, leaf litter, sand, gravel, or rocks at substrate level at 1-m intervals. Rocks were scored by their size as rock 1 (<25 cm diameter), rock 2 (between 25 and 50 cm), or rock 3 (>50 cm). Using the same procedure, we recorded plant contacts with the stick at heights of 5, 10, 25, 50, and 100 cm. This procedure provided 16 sample points per individual that allowed us to calculate for each observation the values of 12 habitat variables in the area surrounding the amphisbaenian (i.e., number of contacts with each substrate and vegetation type, and with vegetation at each height). The sampling of multiple points to characterize surfaces near the amphisbaenians rather than only measuring the particular point at the amphisbaenian location allowed a better characterization of the microhabitat in the home range of an amphisbaenian (for a similar sampling methodology see Scheibe 1987; Martín and López 1998). We also measured thickness and width of stones used by amphisbaenians, the distance from the point of capture to the nearest large rock (>1 m diameter), and the distance from the point of capture to the nearest trunk of a bush.

For each observation, we also recorded date, time of day, age (adults vs. juveniles), sex of adults (determined by presence or absence of hemipenes), snout–vent length (SVL), and body mass. For analysis of ontogenetic variation in microhabitat selection, we considered three categories of SVL (males: 142 ± 3 mm (mean \pm SE), range = 113–165 mm, $n = 24$; females: 140 ± 3 mm, range = 120–172 mm, $n = 23$; juveniles: 93 ± 4 mm, range = 73–119 mm, $n = 13$) and body mass (males: 5.7 ± 0.3 g, range = 3.2–9.7 g; females: 5.5 ± 0.4 g, range = 2.7–10.4 g; juveniles: 1.8 ± 0.2 g, range = 0.5–3 g).

Given the large size of the area surveyed, the high amphisbaenian density, and because we avoided walking routes taken previously, the probability of repeated sampling on the same individual was very low. We therefore treated all measurements as independent.

Availability of different kinds of microhabitat 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. The same procedure was followed for measuring microhabitat values as when encountering an amphisbaenian (i.e., 16 sample points per location that allowed us to calculate the values of 12 habitat variables).

We performed principal component (PC) analysis to reduce the 12 habitat variables to a smaller number of independent components. Original data (number of contacts) were normalized by a square-root transformation. Only factors that accounted for more than 10% of the variance were retained for further analyses, and the initial factorial solutions were rotated by the varimax procedure (Nie et al. 1975). We used PC scores to determine if amphisbaenians

Table 1. Microhabitats measured in the field from randomly determined points and used by *Trogonophis wiegmanni*.

	<i>T. wiegmanni</i> (<i>n</i> = 60)	Random (<i>n</i> = 36)
Ground level		
Gravel	2.6±0.4	2.4±0.5
Sand	4.0±0.3	4.2±0.5
Leaf litter	5.2±0.4	3.9±0.7
Grass	1.2±0.2	1.5±0.4
Rock 1	2.1±0.2	3.3±0.4
Rock 2	0.2±0.1	0.3±0.1
Rock 3	0.4±0.1	0.4±0.2
Plant cover		
5 cm high	7.8±0.4	6.5±0.6
10 cm high	7.7±0.3	6.1±0.5
25 cm high	6.9±0.3	6.5±0.7
50 cm high	4.0±0.4	3.7±0.7
100 cm high	1.8±0.3	1.3±0.4
Distance to rock (cm)	292±16	287±24
Distance to bush (cm)	47±6	75±13
Rock width (cm)	31±2	25±4
Rock thickness (cm)	10.5±1	15.3±2

Note: Values are means ± 1 SE (see Materials and methods).

used available microhabitats in a nonrandom fashion (for a similar procedure see Martín and Salvador 1997; Martín and López 1998). We compared the distribution of amphibaenian microhabitat PC scores with the corresponding PC scores of available microhabitats by using one-way ANOVAs (Sokal and Rohlf 1995). We also used one-way ANOVAs to examine differences between the sexes and size classes.

Results

The structural characteristics of the microhabitats occupied by amphibaenians and those obtained from randomly selected points are shown in Table 1. The PC analysis for microhabitat characteristics produced three components that together accounted for 61.1% of the variance (Table 2). The first factor (PC 1) accounted for 30% of the variance and showed a positive correlation with vegetation that was 25, 50, and 100 cm high and leaf litter, and was negatively correlated with sand (i.e., it represented a gradient from open sandy areas to vegetated areas that were 25–100 cm high and composed of the perennial bushes *A. halimus*, *S. oppositifolia*, and *L. intricatum*) with leaf-litter substrate. The second factor (PC 2) accounted for 18.6% of the variance and showed a positive correlation with 5 and 10 cm high vegetation cover and was negatively correlated with small stones (rock 1) (i.e., it described a gradient from open areas with abundant small stones to areas with 5–10 cm high vegetation cover composed of perennial low shrubs such as *A. halimus*, *L. intricatum*, and *S. vera* and herbs such as *Lavatera mauritanica* and *Malva parviflora*). The third factor (PC 3) accounted for 12.5% of the variance and described a gradient of types of substrate from areas with gravel and small stones to areas with leaf litter.

Amphibaenians did not use microhabitats in proportion to their availability (Fig. 1). Amphibaenians occupied

Table 2. Principal component (PC) analysis for randomly determined points and amphibaenian microhabitat data.

	PC 1	PC 2	PC 3
Ground level			
Sand	-0.46	0.15	0.14
Gravel	0.01	-0.06	-0.90
Leaf litter	0.45	0.17	0.76
Grass	-0.25	0.20	0.36
Rock 1	0.13	-0.53	-0.45
Rock 2	-0.03	-0.03	0.06
Rock 3	-0.11	0.12	-0.02
Plant cover			
5 cm high	0.05	0.95	0.01
10 cm high	0.29	0.89	0.16
25 cm high	0.72	0.33	0.39
50 cm high	0.92	0.10	0.16
100 cm high	0.84	-0.003	-0.11
Eigenvalue	3.59	2.23	1.50
Percent variance	30.0	18.6	12.5

Note: Values that are correlated and contribute significantly to the PC scores are in boldface type.

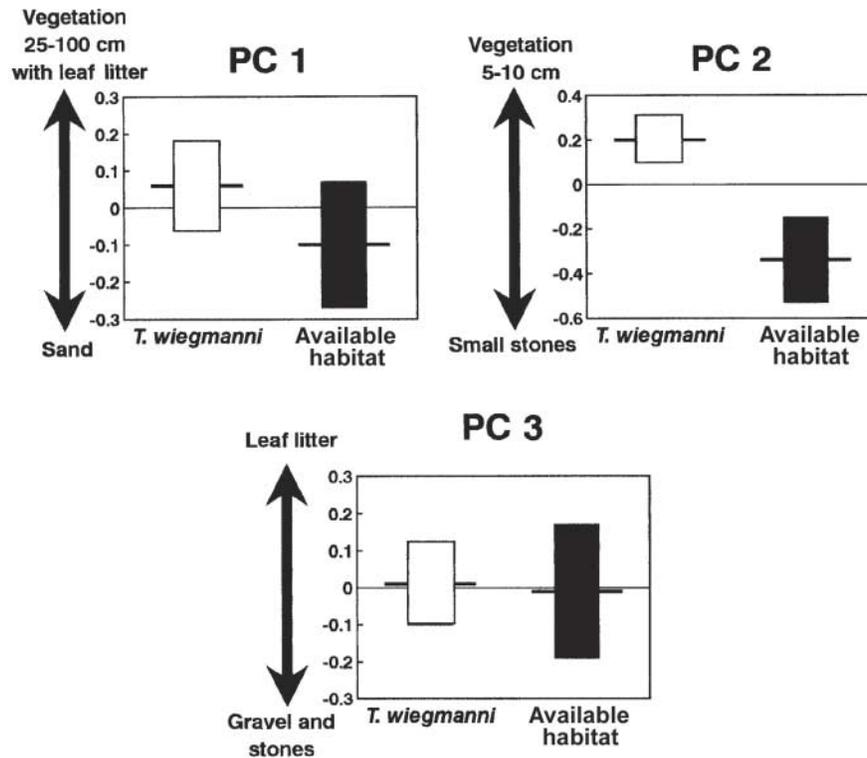
microhabitats with higher scores on PC 2 (ANOVA, $F_{[1,94]} = 7.18$, $P = 0.009$). However, microhabitats defined by PC 1 and PC 3 were used by amphibaenians in proportion to their availability (ANOVA; PC 1: $F_{[1,94]} = 1.4$, $P = 0.24$; PC 3: $F_{[1,94]} = 0.013$, $P = 0.90$; Fig 1). Thus, amphibaenians preferentially used sites with vegetation cover that was 5–10 cm high and less open areas with small stones.

On the other hand, amphibaenians were found under rocks that were significantly thinner (ANOVA, $F_{[1,94]} = 4.27$, $P = 0.041$), wider (ANOVA, $F_{[1,94]} = 8.96$, $P = 0.004$), and closer to bushes (ANOVA, $F_{[1,94]} = 4.61$, $P = 0.034$) than those measured at randomly selected points (Table 1). The only variable that differed significantly between the sexes and age classes was PC 3 (ANOVA, $F_{[2,59]} = 4.22$, $P = 0.019$). Tukey's HSD post-hoc tests showed that PC 3 differed significantly ($P = 0.037$) between males ($n = 24$, 0.34 ± 0.16) and juveniles ($n = 13$, -0.53 ± 0.3), but not between females ($n = 23$, -0.01 ± 0.18) and juveniles ($P = 0.33$) or between males and females ($P = 0.31$). Thus, males tended to use microhabitats with more leaf litter than juveniles, which tended to use more gravel substrates with small stones than males. Additionally, juveniles tended to be found under thinner stones (7.5 ± 1.4 cm) than adults (11.4 ± 1.24 cm; ANOVA, $F_{[1,58]} = 3.93$, $P = 0.052$). We also found significant correlations of SVL with rock thickness ($r_s = 0.30$, $P = 0.02$), rock width ($r_s = 0.35$, $P = 0.05$), distance to nearest rock ($r_s = 0.26$, $P = 0.042$), and PC 3 ($r_s = 0.41$, $P = 0.001$). Thus, larger amphibaenians occupied habitats with larger rocks that were placed closer to large rocks and in areas with leaf litter and 25 cm high grass.

Discussion

Our results show that *T. wiegmanni* used microhabitats in proportion to their availability with one exception: they showed a preference for areas with 5–10 cm high vegetation cover (i.e., perennial bushes and scrubs such as *A. hali-*

Fig. 1. Mean (± 1 SE) values of the principal component scores for microhabitats used by *Trogonophis wiegmanni* (open boxes) and for available habitat at randomly selected sites (solid boxes).



mus, *L. intricatum*, and *S. vera* and herbs such as *L. mauritanica* and *M. parviflora*) and avoided areas with abundant small stones. These results indicate that at least some structural characteristics of the microhabitat occupied by amphisbaenians seem to be different from those of readily available habitats. This nonrandom association may result from ecological requirements of amphisbaenians inhabiting dry environments.

Amphisbaenians use stones as daytime refuges where they can thermoregulate without being exposed to predators on the surface (Martín et al. 1990, 1991). Relative humidity is higher beneath stones, and potential prey are found sheltering there. Vegetation cover provides shade, permitting behavioral thermoregulation for amphisbaenians (Martín et al. 1990). The vegetation in these islands consists mainly of perennial shrubs, herbs, and grass. Amphisbaenians were found more often under rocks in areas of 5–10 cm high vegetation cover and closer to bushes than in all readily available habitats. This vegetation cover might allow an equilibrium between maintaining the humidity in the substrate (making the soil easier for burrowing or just because in dry environments humidity is important per se) and sun exposure of the rocks used by amphisbaenians. Additionally, most plants 5–10 cm high are herbs, and soils containing herb roots retain an excess of water that in dry environments may be very important for amphisbaenians. In contrast, rocks in open areas without vegetation are directly exposed to the sun, which may cause overheating, and amphisbaenians might suffer heat stress. Thus, the presence of overhanging vegetation at these sites may reduce the net radiation intake and keep high moisture levels, and hence cool ambient temperatures.

Interestingly, *T. wiegmanni* used microhabitats defined by PC 1 (vegetation cover of bushes 25–100 cm high with abundant leaf litter under them) in proportion to their availability. In contrast, a previous study with the amphisbaenian *Blanus cinereus* suggested that this species preferred areas with abundant leaf litter from bushes of *Juniperus* sp. because digging was easier here, but also because leaf litter was associated with a layer of humus that was a source of invertebrate food (Martín et al. 1991). However, in our study area, characterized by little precipitation and high temperatures, the leaf-litter layer of the bushes present is too dry and sparse; hence, the soil under the leaf-litter layer is dry and compacted, making digging difficult.

Our data show that amphisbaenians select rocks of different sizes. Such choices could have important thermoregulatory consequences. *Trogonophis wiegmanni* selected thinner and wider rocks than those rocks found randomly in the study area. It can be advantageous for ectotherms to shelter under rocks for long periods, since they can easily maintain their preferred temperature at little energy cost (Huey et al. 1989). They could obtain heat from the rocks to increase their body temperature without being exposed on the soil surface, thus minimizing predation risk. The thermal suitability of rocks depends on their thickness and their exposure to the sun (Huey et al. 1989). López et al. (1998) showed that the amphisbaenian *B. cinereus* avoided the thinnest rocks, probably to avoid heat stress at midday. However, our results show that *T. wiegmanni* used thinner rocks instead of all available rocks. This might suggest that in warmer habitats occupied by *T. wiegmanni*, better thermoregulatory opportunities may allow them to achieve higher body temperatures (Al-Johany 1999). This suggests that

amphisbaenians living in warmer areas might be adapted to tolerate a higher critical thermal maximum than amphisbaenians occupying temperate habitats. However, there is a lack of evidence on thermal limitations of this species, so further studies are necessary to test this hypothesis. Additionally, in our study area soils are little developed and thicker rocks have little or no soil under them. Thus, amphisbaenians are probably not able to dig under them.

Trogonophis wiegmanni also used wider rocks than expected. One possible explanation to the use of wider rocks in dry environments is that the relative humidity is higher beneath the wider rocks and potential prey are found sheltering there. Therefore, the wider the rocks, the higher the humidity and the higher the abundance of potential prey. However, it is unclear if these sites are occupied because they provide the best thermal conditions or because they offer an abundance of food. Interestingly, larger individuals occupied thinner and wider rocks that were placed closer to large rocks in areas with leaf litter and 25 cm high grass. This supports the idea that thinner and wider rocks may provide the best thermal and food conditions.

Our study failed to find differences in habitat selection between the sexes. The lack of intrasexual differences in microhabitat selection could be a consequence of the homogeneity of the underground environment, but it also could be due to the lack of sexual dimorphism in morphology. If adult males and females have similar ecological requirements, they would be expected to show similar patterns of habitat selection.

Concerning differences in microhabitat selection among age classes, juveniles used more gravel substrates with more small stones than males, but there were no differences between juveniles and females. Although this might reflect juvenile avoidance of males, this can also be just a biophysical effect of differences in body size. Additionally, juveniles tended to be found under thinner stones than adults, suggesting that smaller rocks might supply the thermal and food requirements of smaller individuals but not those of larger individuals, which will select larger and wider rocks. Alternatively, intraspecific competition might also occur with large individuals inhabiting the best microhabitats.

In conclusion, our data show that amphisbaenians, in spite of locomotory restrictions imposed by their burrowing life, did not use all microhabitats in proportion to microhabitat availability. They showed a preference for areas with 5–10 cm high vegetation cover and avoided areas with an abundance of small stones. Our data also show that *T. wiegmanni* selected thinner and wider rocks than those found randomly. This capacity to select specific microhabitats where thermal and food requirements are probably better satisfied in the underground environment would be evolutionarily advantageous and is likely to represent a component of the suite of adaptations associated with fossoriality.

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