

# Coping with drought? The hidden microhabitat selection and underground movements of amphisbaenians under summer drought conditions

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## Abstract

Habitat selection is a dynamic process that depends on many environmental variables that can vary with weather conditions. This is important because, within a context of global change, extreme weather events, such as severe droughts, are predicted to become more frequent. We examined the patterns of microhabitat selection and underground movements (using PIT-tag telemetry) of a strictly fossorial reptile, the North African checkboard amphisbaenian *Trogonophis wiegmanni*, during the summer drought period. We aimed to test whether changes in strategies of habitat use and movements could allow this amphisbaenian to cope with unfavorable weather. We found that during the summer drought period, *T. wiegmanni* did not use the microhabitats in relationship to their availability, but particularly selected sites with high abundance of rocks but also areas under a high cover of bushes, where environmental conditions were more favorable. We also found, using PIT-tag telemetry, that the numbers of *T. wiegmanni* individuals located under rocks and their activity (number of days with movements) decreased largely in summer. However, the animals were not entirely inactive, but, especially males were active below the ground under bushes and made some relatively long underground hidden movements between favorable areas.

**Key words:** arid environments, fossoriality, habitat selection, movement ecology, *Trogonophis wiegmanni*, weather conditions.

Understanding the habitat requirements of animals is an important objective not only to expand our basic ecological knowledge (Schoener 1977; Manly et al. 2002; Stamps 2009) but also for wildlife management and the design of adequate conservation plans (Scott et al. 2002; Guisan and Thuiller 2005). Hence, numerous studies have used a diversity of techniques to examine the habitat selection patterns of many types of animals (e.g., Heatwole 1977; Cody 1985; Harris and Davies 2010). The selection of an optimal habitat is a dynamic process that depends on many variables such as physical and physiological constraints, resource availability, predation risk, and/or reproductive opportunities (e.g., Huey 1991; Pringle et al. 2003; Paterson and Blouin-Demers 2018), all of which can also vary temporarily with, for example, weather conditions (Van Beest et al. 2012; Sunde et al. 2014; Mayer et al. 2019).

The effect of weather is important within a context of global change, because extreme weather events, such as heat waves or extreme droughts, “have already become more frequent in recent times” (Coumou and Rahmstorf 2012). For example, Mediterranean arid regions experience a typically dry and hot summer period that typically lasts for around 3 months (June–September) (Lionello 2012). These climatic conditions negatively affect many animals, for example, by decreasing food availability (Sperry and Weatherhead 2008; Martín et al. 2023) or, especially in ectothermic animals, by inducing thermal and hydric stress (Diele-Viegas and Duarte

Rocha 2018). Many animals seem able to cope with this typical drought period by using different strategies such as migrating temporally to localities with better habitat conditions (Abraham et al. 2019) or estivating in retreats (Secor and Lignot 2010). However, it is relatively little known whether and how animals respond to the negative effects of unusual extreme weather conditions, such as an extended drought period. Therefore, it is important to understand the strategies of habitat use and behavior of animals that could allow them to cope with drought, and whether these strategies might be useful enough to respond to the foreseen increase in extreme weather conditions.

Fossorial species of vertebrates, such as some mammals, skinks, amphisbaenians, or caecilians spend most of their lives underground (Gans 1978; Lacey et al. 2000) and, in many cases, are quite sedentary, with low dispersal ability (e.g., Martín et al. 2021). Hence, fossorial species may be particularly affected by adverse weather conditions. These effects may be, either direct (e.g., hydric stress) or indirect, due to the soil alterations, such as increased compaction, derived from these dry conditions (Tibbett et al. 2020). However, the fossorial animals are generally understudied (Guedes et al. 2023) and the potential negative effects of the altered environment on their ecology and conservation state often remain unnoticed (Colli et al. 2016). Moreover, the study of fossorial animals has obvious methodological difficulties derived from the technical problem of finding

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and following the always hidden individuals without disturbance. For example, sampling techniques for fossorial reptiles are often based on active searching by digging or by lifting rocks or artificially provided cover boards (Measey 2006; Henderson et al. 2016). However, digging can disturb the animals and the habitat, while fossorial animals are not always living under rocks. For example, during hot and dry periods, fossorial animals might move deeper or to cooler or moister soils away from rocks. Therefore, surveys based on these techniques alone and restricted to some particular sites (e.g., under rocks) might impede or bias the observations of ecology and behavior of these animals. In the last years, some research of fossorial vertebrates has used passive integrated transponder (PIT) telemetry (i.e., detecting at a distance the radiofrequency signal of PIT-tag-marked buried individuals) (Gibbons and Andrews 2004). This technique is used to detect and follow individuals underground without disturbance (Kuhn 2000; Connette and Semlitsch 2012; Ousterhout and Semlitsch 2014; Martín et al. 2021) and may also allow examining without bias their behavior and ecological requirements.

Among fossorial animals, amphisbaenian reptiles are one of the most characteristic groups. They are highly adapted to an underground life-style (Gans 1978; Navas et al. 2004), but little conspicuous and, hence, highly understudied. In the few amphisbaenian species examined, the selection of microhabitats is not random but based on soil characteristics, such as choosing sandy loose substrates or with abundant leaf litter, where digging may be less costly and body water loss may be lower (Martín et al. 1991, Martín, López, et al. 2013; Civantos et al. 2003). These amphisbaenians also often prefer areas with a high cover of rocks, under which they can thermoregulate, and find a relatively high humidity and more abundant invertebrate prey (Martín et al. 1990, Martín, Ortega, et al. 2013; López et al. 1991, 1998, 2002). However, these studies were made in seasons with optimal weather conditions and based on observations of animals found under lifted rocks. It remains to be examined how the summer drought period affects these patterns of microhabitat selection and whether the type of survey method can bias the observed results.

Here, we examined the patterns of microhabitat selection and underground movements of the checkboard amphisbaenian *Trogonophis wiegmanni*, a species that inhabits North Western African arid regions (Bons and Geniez 1996). Field observations indicate that these amphisbaenians are less often found under rocks when the weather is hot and dry and prey availability under rock decreases (Martín et al. 2023), initially suggesting that they may simply move to deeper areas in the soil entering into a state of aestivation and interrupting all activity (Bons and Saint-Girons 1963). However, the actual space use and activity patterns of *T. wiegmanni* amphisbaenians during the summer dry season have not been studied. We used 2 different methodologies to locate animals (lifting rocks vs. telemetry of PIT-tag marked individuals). We specifically tested whether, in response to drought conditions, this amphisbaenian is able 1) to use specific microhabitats differentially in relation to the expected by their availability and 2) to decrease activity or adopt particular underground movement strategies. Additionally, we compared 3) whether the results of habitat selection studies differed depending on the survey technique used.

## Materials and Methods

### Study area and sampling procedures

We carried out the study from 16th to 29th June 2022 at Isabel II Island, a small island (15.1 ha) belonging to the Chafarinas Archipelago (Spain). These islands are located in the Mediterranean Sea (35°11'N, 02° 25'W) offshore the Moroccan coast. Soils in these islands are immature and little developed, with a thin horizon rich in organic matter of around 12 cm mean depth, which is practically directly placed over volcanic rocks (García 2005). The vegetation of Isabel II Island mainly consists of woody bushes *Salsola oppositifolia* and herbaceous grasses adapted to soil salinity and drought, which are consequences of the warm arid Mediterranean climate (García et al. 2002). In these Islands, *T. wiegmanni* maintains large populations (Martín et al. 2011a; 2011b).

We had delimited a study plot in Isabel II Island (plot area = 0.14 Ha), following geographical feature limitations, that comprised an area with homogeneous habitat conditions (a mosaic of abundant medium-sized volcanic rocks and *Salsola* bushes on sandy substrates) (Figure 1). This habitat is optimal for amphisbaenians (Martín, López, et al. 2013), allowing them to occupy all the surface of the plot. We have monitored the population of *T. wiegmanni* in this plot since 2015 by making two campaigns of marking-recapture per year. For the current study, we surveyed systematically and intensively the entire plot every day, searching for amphisbaenians by lifting almost all rocks of a size that would allow holding an amphisbaenian under them (Civantos et al. 2003). We captured live amphisbaenians by hand and measured their snout-to-vent length (“SVL”; from the tip of the snout to the extreme posterior point of the cloacal flap) with a metallic ruler (to the nearest 1 mm) and body “mass” with a digital scale (to the nearest 0.01 g). We determined the sex of individuals by examining the presence of hemipenes in the cloacae (Martín et al. 2011b, 2012).

We marked amphisbaenians at first capture by implanting PIT tags (8.4 mm × 1.4 mm; Biomark MiniHPT8; Biomark, Inc., Boise, ID, USA) subcutaneously in the upper right side of the body (for details and validation of the procedure see Recio et al. 2019). The weight of a PIT-tag (0.03 g) represents around 0.6% of the mean body mass of a typical adult amphisbaenian in our population (Martín et al. 2011b), which ensured that the PIT-tag did not interfere with the locomotion of amphisbaenians. When an amphisbaenian was found, we first confirmed whether the individual was already marked using a hand-held portable reader (Biomark 601 Reader) to read the individual unique code of the tag. This is because many individuals in this plot had been already marked during marking campaigns made in previous years (e.g., Martín et al. 2021). If the individual was unmarked, we followed the marking procedure. The location of each individual was determined using a GPS (GPSmap 62st; Garmin Ltd., Olathe, KA, USA), which had been previously calibrated with respect to reference points of the plot in each session to decrease measurement error. Thereafter, we released amphisbaenians at their exact point of capture, less than 5 min after finding them.

### PIT telemetry

Simultaneously to the rock surveys made as above, another researcher performed morning and afternoon daily surveys of the entire surface of the study plot using an HPR Plus Reader equipped with a BP Plus Lite Portable Antenna (Biomark, Inc., Boise, ID, USA). This reader allowed telemetry detection





**Figure 1.** Microhabitats at the Chafarinas Islands during the summer drought. View of the study plot showing large open areas of bare soil with gravel, groups of medium-sized rocks, and scattered *Salsola* bushes. Small surveying red flags mark the locations of individual amphisbaenians detected using PIT-tag telemetry. Inserted (bottom left) is a picture of an amphisbaenian (*Trogonophis wiegmanni*) as it was found under a rock.

of PIT tags of marked amphisbaenians while they remained buried at any place under the ground surface. This method avoids any possible disturbance to individuals, which do not need to be located under lifted rocks (Martín et al. 2021; for the use of this method in other fossorial animals see Kuhnz 2000; Connert and Semlitsch 2012; Ousterhout and Semlitsch 2014). Preliminary trials showed that the 8.4 mm PIT tags that we used could be detected buried up to about 20 cm deep and also under rocks up to about 10 cm height without lifting them (unpublished data; see also Ousterhout and Semlitsch 2014).

In each session, the study plot was surveyed in a linear search pattern beginning at the southern end and moving slowly to the northern side of the plot. While searching, we slowly swung the antenna from side to side, giving sufficient overlap to cover the ground completely. The entire surface plot was searched as thoroughly as possible, searching in all open ground, rocky areas, and by inserting the antenna below the bushes at ground level. After the signal of a PIT-tag marked amphisbaenian was detected underground, the exact individual's position was determined carefully. The location in the plot was determined with the GPS and marked with a surveying flag (labeled with the tag number) that remained in the plot as a reference during all the surveys.

### Habitat selection

We examined characteristics of microhabitats used by *T. wiegmanni* in the study plot using 2 different methods. We

first 1) made surveys “restricted to rocks” lifted and measured microhabitats (see below for details) in the area immediately surrounding the rock where we actually found an individual amphisbaenian (“microhabitat used”). Then, we compared these data with a random survey of the microhabitats around the available rocks in the entire study plot that could potentially contain amphisbaenians (i.e., rocks with a size and dimensions similar to the ones used by amphisbaenians; Civantos et al. 2003) (“microhabitat available”). We also 2) made surveys at “any place” across the entire study plot surface (including open areas, rocks, and bushes) using PIT telemetry (see above) to detect the presence of buried amphisbaenians at any site (“microhabitat used”) in comparison with “available microhabitats” randomly determined at any place across all the entire plot.

In both types of surveys, we characterized microhabitat use by amphisbaenians the first time that we found a given individual either under a lifted rock or by detecting the signal of its PIT tag at any place. We took four 50 cm transects, one at each of the 4 cardinal directions radiating from the rock or point where each individual was found or located. We used a scored stick standing vertically at 8 sample points (2 points at 25-cm intervals in each of the four transects) and recorded the contacts with the stick at the ground level of “gravel and small rocks” (2–5 cm length) and “medium sized rocks” (5–60 cm), “bare soil,” “leaf litter,” (from bushes) and “grass” (mainly dry remains of annual herbs). We also noted contacts of the *Salsola* bushes (the only woody species found in the plot) with the stick at 5, 10, 25,

50, and 100 cm height (Table 1). This procedure allowed the characterization of each microhabitat variable in the area surrounding each amphisbaenian location (i.e., number of contacts with each substratum type and with vegetation at each height; for a similar sampling methodology see Martín and López 2002). The availability of microhabitats in the study plot was estimated along a series of random transects covering the whole plot. Every 5 m, we marked a point and followed the same procedure as when encountering amphisbaenians to measure microhabitat variables at the transect point (“any place”) and also at the nearest rock (“restricted to rocks”) to that transect point as the centers of two sampling areas.

We used principal component analysis (PCA) to reduce the 10 microhabitat variables (see Table 1) to a smaller number of independent principal components (PCs). Original data (number of counts) were subjected to square-root transformation to ensure normality. The initial factorial solution was rotated by the Varimax procedure to maximize the variance on the new axes and to show a clear pattern of factor loadings (Tabachnick and Fidell 2007). For further analyses, we only used the PCs with eigenvalues greater than one. Then, we used two-way analyses of variance (ANOVAs) to analyze separately whether the microhabitat characteristics defined by each of the PC scores (response variables) differed between sites “available” and “used” by amphisbaenians (fixed categorical factor), and between observations made at “any place” of the plot or “restricted to rocks” (fixed categorical factor), and included the interaction between these 2 factors in the models (Sokal and Rohlf 1995). To examine whether there were sexual or body size-related differences in habitat use, we made separated 3-way ANOVAs for each of the PC scores restricted to the microhabitats used by amphisbaenians, including the “survey method” (any place vs. restricted to rocks), “sex” (both as categorical fixed factors), and “body size” (SVL) of the individuals (continuous fixed covariate)

and including all the interactions between the 3 factors in the models.

### Underground movements

We used PIT telemetry (see above) to study daily underground movements of individual amphisbaenians that had been marked with PIT tags in previous campaigns made in the study plot. As tracked individuals remained underground and were not handled or disturbed by us during these PIT telemetry surveys, we considered that they were moving freely, independently of our repeated surveys. After the initial detection (see above), during each subsequent survey, we tracked and tried to find again all previously detected individuals. If an amphisbaenian was found at the previous location (marked with a flag and tag number), we considered that it had not moved since the previous survey. If an amphisbaenian was not found at its previously known location, we searched for it with the antenna, starting at the last point where it was detected and following a circular pattern. If the individual had moved and was later detected, the shortest lineal distance from the previous to the current position was measured with a metric tape to the nearest cm. The flag was repositioned to the new location and the time spent between successive relocations was later calculated. When an individual was not detected in a circle of 3-m radius circle around the last known point, we considered that it had moved far away, and was noted as temporarily missed. However, while we continued searching in the plot, we often detected elsewhere the signal of some previously located but missed individuals. Then, the distance and direction to the previous location were measured, and its flag was repositioned. When we found new marked individuals who had not been detected in any of the previous days, they were incorporated to the study and followed in posterior surveys.

**Table 1.** Microhabitats available and used by the amphisbaenian *Trogonophis wiegmanni* at the Chafarinas Islands

	Available		Used by <i>T. wiegmanni</i>	
	Any place ( <i>n</i> = 40)	Rock ( <i>n</i> = 40)	Any place ( <i>n</i> = 52)	Rock ( <i>n</i> = 31)
Substrate contacts				
Gravel and small rocks	3.4 ± 0.4	2.2 ± 0.3	2.3 ± 0.3	0.7 ± 0.2
Medium-sized rocks	1.5 ± 0.3	3.0 ± 0.3	3.0 ± 0.3	4.1 ± 0.2
Bare soil	2.9 ± 0.3	2.6 ± 0.2	2.0 ± 0.2	2.6 ± 0.2
Leaf litter	0.1 ± 0.1	0.0 ± 0.1	0.6 ± 0.2	0.4 ± 0.1
Grass	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.1
Vegetation contacts at height				
5 cm	0.1 ± 0.1	0	0.5 ± 0.2	0.1 ± 0.1
10 cm	0.6 ± 0.2	0.7 ± 0.1	2.9 ± 0.3	0.5 ± 0.2
25 cm	1.0 ± 0.2	1.4 ± 0.2	5.0 ± 0.3	1.9 ± 0.3
50 cm	0.5 ± 0.1	0.8 ± 0.2	4.4 ± 0.3	1.4 ± 0.3
100 cm	0.1 ± 0.1	0.2 ± 0.1	2.4 ± 0.3	0.5 ± 0.2

Variables (mean ± SE of the number of contacts) that characterize microhabitats available and used by amphisbaenians when considering observations at “any place” of the study plot or “restricted to rocks.” Sample sizes (*n*) refer to the number of sampling points or individuals surveyed in each category for which we characterized microhabitats.



**Table 2.** Relationships between microhabitat variables at the Chafarinas Islands

	PC-1	PC-2	PC-3	PC-4
Substrate contacts:				
Gravel and small rocks	0.03	<b>-0.92</b>	-0.16	0.26
Medium-sized rocks	0.15	<b>0.84</b>	-0.31	0.18
Bare soil	-0.26	0.22	0.13	<b>-0.80</b>
Leaf litter	0.28	0.10	<b>0.81</b>	-0.03
Grass	-0.35	0.06	0.15	<b>0.73</b>
Contacts with <i>Salsola</i> bushes at height:				
5 cm	0.09	-0.13	<b>0.89</b>	0.02
10 cm	<b>0.65</b>	-0.03	0.37	-0.06
25 cm	<b>0.90</b>	0.05	0.22	-0.07
50 cm	<b>0.92</b>	0.06	0.11	0.01
100 cm	<b>0.80</b>	0.02	-0.04	0.16
Eigenvalues	3.34	1.77	1.57	1.11
% Variance explained	33.4	17.7	15.7	11.1
Cumulative % variance	33.4	51.1	66.8	77.9

PC analysis for variables describing microhabitats available and used by *T. wiegmanni*, when considering observations at any place of the study plot and restricted to rocks. Correlations in bold lettering correspond to variables sharing at least 30% variance with the components, according to [Tabachnick and Fidell \(2007\)](#).

We calculated the movements (to the nearest 1 cm) of individuals found elsewhere in the plot at least twice after their first detection while they remained underground and undisturbed. To analyze these movements, given the right skewed non-normal distribution of data, we used 3 different generalized linear models (GLMs), with a Poisson distribution and a log link function, with the dependent variable being either 1) the mean “distance moved per day” (calculated considering the total number of survey days that the individual was followed, including those without apparent movements), 2) the “percentage of days with movements,” or 3) the mean “distance of the movements per day” considering only the days in which a meaningful movement occurred (i.e., excluding days without apparent movements). We included in the models the “sex” as an explanatory categorical fixed factor, “body size” (SVL) as a continuous fixed covariate, and the interaction between “sex” and “body size.” When this interaction was significant, we made further separated GLM models for males and females to explore the meaning and direction of such interaction.

To examine the habitat use of amphisbaenians during these surveys, we also noted for each location whether the buried amphisbaenian had been located under rocks, under the cover of *Salsola* bushes, or into open soil (either with bare soil and gravel or herbs, but without bush cover). We calculated for each individual the percentage of locations in each habitat type and used these data from all individuals to calculate the means of locations in each habitat. We used a Chi-squared test to compare these data with the availability of these 3 categories of microhabitats estimated from an aerial picture of the study plot taken in the same month. Comparisons between sexes were made with Mann–Whitney *U* tests, and relationships with body size estimated with Spearman rank order correlations. Statistical analyses were made with the Statistica 8.0 software (StatSoft Inc., Tulsa, OK, USA).

## Results

### Microhabitat selection

We gathered information on microhabitats used by 83 individual *T. wiegmanni*, that were either found under rocks (10 males with a mean  $\pm$  SE SVL of  $133 \pm 6$  mm; 21 females, SVL =  $129 \pm 3$  mm) or detected using PIT-tag telemetry (28 males, SVL =  $139 \pm 3$  mm; 24 females, SVL =  $137 \pm 3$  mm). We compared these data with available microhabitats measured at “any place” in random transects ( $n = 40$  points) and “restricted to the rock” found nearest to each transect point ( $n = 40$  points). Average characteristics of microhabitats available and used by *T. wiegmanni* are described in [Table 1](#). The PCA produced 4 PCs with eigenvalues  $>1$  that together accounted for 77.9 % of the variance ([Table 2](#)). The first PC (PC-1) described a gradient from microhabitats without bushy vegetation in the negative side to microhabitats with a high cover of *Salsola* bushes in the positive side. The second PC (PC-2) was interpreted as a gradient from microhabitats with high cover of gravel and small rocks to microhabitats with high cover of medium-sized rocks. The third PC (PC-3) represented a gradient toward microhabitats with high cover of leaf litter under small bushes of low height. Finally, the fourth PC (PC-4) described a gradient from microhabitats with high cover of bare soil to microhabitats with increasing grass cover.

There were some significant differences between microhabitats available and used by *T. wiegmanni*, but there were also differences when comparing microhabitats measured at any place of the plot with only those restricted to rock observations ([Table 3](#)). Thus, the significant interaction for PC-1 factor scores showed that amphisbaenians used significantly more often than expected by their availability microhabitats under high cover of *Salsola* bushes, but this difference was only significant when locations at any place of available and used microhabitats were considered (Tukey’s test,  $P < 0.0001$ ), but not when observations of available and used

microhabitats were restricted to rocks ( $P = 0.72$ ) (Table 3 and Figure 2A).

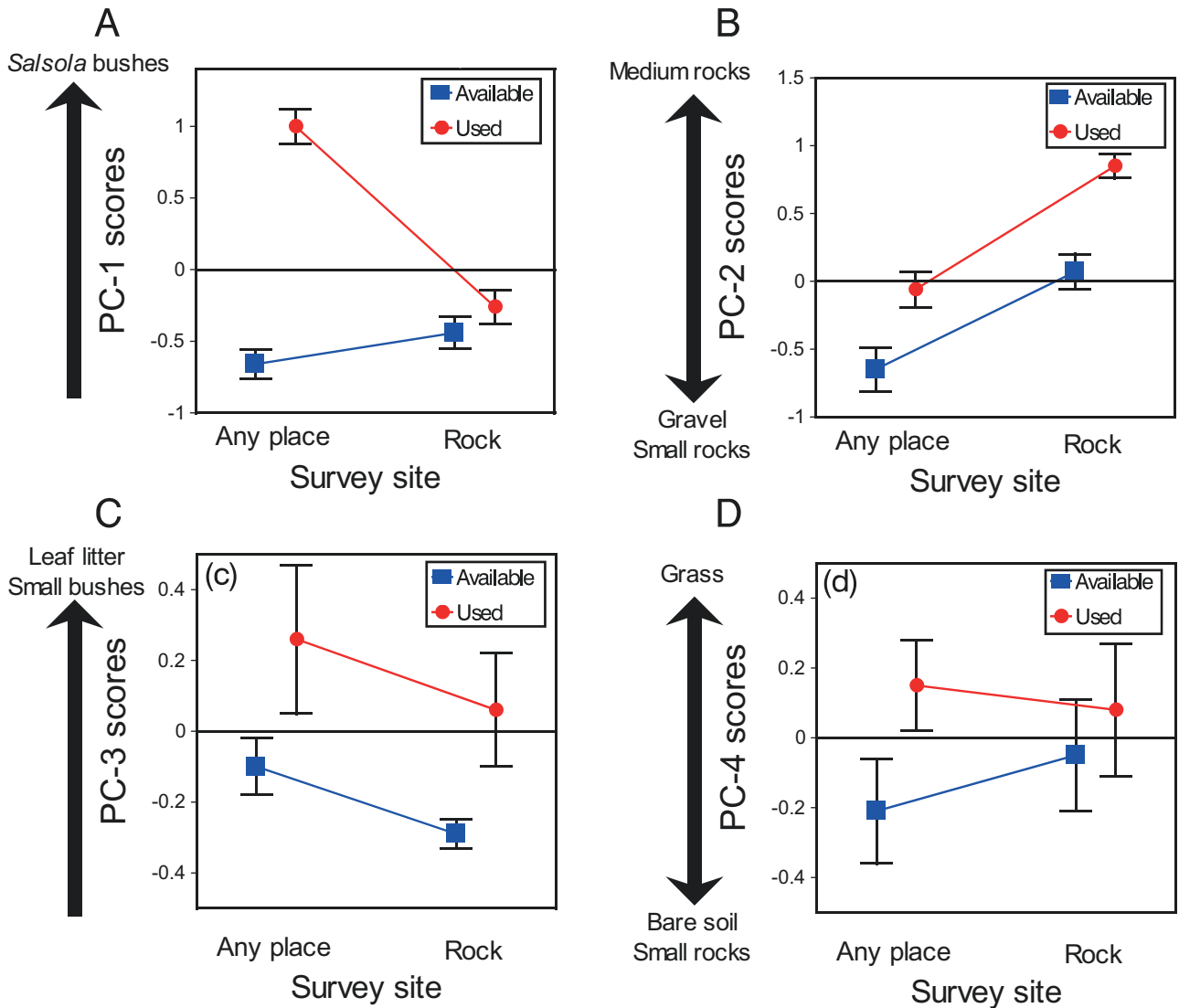
Examination of results for PC-2 scores showed that amphisbaenians used medium-sized rocks significantly more often than expected by their availability (Table 3 and Figure 2B),

independently of the type of survey made to sample microhabitats (i.e., the interaction was not significant), although surveys restricted to rocks offered significantly higher values of cover of medium-sized rocks (both for available and used sites) than if surveys were made at any place.

**Table 3.** Microhabitat selection by the amphisbaenian *T. wiegmanni*

	PC-1			PC-2		PC-3		PC-4	
	<i>df</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Available versus Used	1	63.68	<0.0001	24.24	<0.0001	5.16	0.02	2.40	0.12
Any place versus Rocks	1	20.41	<0.0001	33.60	<0.0001	1.60	0.21	0.07	0.79
Interaction	1	40.98	<0.0001	0.46	0.50	0.01	0.99	0.50	0.48
Error	159								

Results (*F*, *P*) of two-way analyses of variance testing differences between microhabitats [defined by the different PC scores] available and used by *T. wiegmanni* amphisbaenians, and comparing microhabitats at “any place” of the study plot with only those “restricted to rock” observations. Significant probabilities are marked in bold.



**Figure 2.** Microhabitat selection by the amphisbaenian *Trogonophis wiegmanni*. Mean ( $\pm$  SE) PC scores from a PCA analysis on all variables describing microhabitats “available” (blue) and “used” (red) by amphisbaenians, and considering microhabitats surveyed either at “any place” of the study plot or only those “restricted to rocks.”

Results for the PC-3 scores showed that amphisbaenians used significantly more than expected microhabitats with high cover of leaf litter and *Salsola* bushes with contacts at low height, independently of the method of sampling (i.e., the interaction was not significant), and the effect of the survey method was not significant (Table 3 and Figure 2C). Finally, with respect to microhabitats with more bare soil or with more grass defined by PC-4 scores, there were no significant differences between available and used microhabitats, or between sampling methods (Table 3 and Figure 2D).

Similar ANOVA analyses restricted to microhabitats used by amphisbaenians, and including the sex and body size of the individuals, did not find, for any of the PCs, any significant difference between sexes ( $P \geq 0.15$  in all cases) or significant relationship with body size ( $P \geq 0.13$  in all cases), and all the interactions were non-significant ( $P \geq 0.19$  in all cases).

### Underground movements

The distance moved underground in successive days by undisturbed amphisbaenians that were followed with the reader was on average ( $\pm SE$ ) of  $65 \pm 11$  cm/day (range = 0–264 cm/day,  $n = 41$  individuals) (Figure 3A). Distances moved by males ( $89 \pm 18$  cm/day, range = 0–264 cm/day,  $n = 22$ ) were significantly longer than those moved by females ( $37 \pm 8$  cm/day, range = 0–110 cm/day,  $n = 19$ ), and there was an overall significant effect of body size ( $Estimate = -0.010 \pm 0.001$ ), but the interaction with sex was significant (Table 4). To explore the meaning of this interaction, we made further separated GLMs for males and females, which suggested that although both smaller males and females moved longer distances than larger ones, this relationship was stronger in females (Males, GLM:  $\chi^2 = 11.66$ ,  $P = 0.0006$ ,  $Estimate = -0.004 \pm 0.001$ ; Females, GLM:  $\chi^2 = 79.48$ ,  $P < 0.0001$ ,  $Estimate = -0.016 \pm 0.002$ ) (Figure 4A).

In many of the relocations of the same individuals, they did not seem to have moved in a meaningful way (i.e., they were at the same location as in the previous survey). Thus, the frequency of days with meaningful movements made by an individual was on average ( $\pm SE$ ) of  $19 \pm 2\%$  (range = 0–50%,  $n = 41$  individuals). Only 7 individuals did not seem to move at all during the study (but mainly because they have a few relocations or were lost and not relocated again when the study had ended), while 23 individuals with more relocations moved less than 20% of days and 18 individuals moved more than 20% of days, although none of them moved more than half of the days (Figure 3B). Males did not move significantly more often ( $18 \pm 3\%$ , range = 0–50%,  $n = 22$ ) than females ( $19 \pm 3\%$ , range = 0–50%,  $n = 19$ ), and smaller individuals moved significantly more often than larger ones ( $Estimate = -0.010 \pm 0.002$ ), but the interaction was significant (Table 4). Separated GLMs showed that this effect of body size was significant in males (GLM:  $\chi^2 = 37.12$ ,  $P < 0.0001$ ,  $Estimate = -0.017 \pm 0.003$ ) but not in females (GLM:  $\chi^2 = 1.29$ ,  $P = 0.25$ ,  $Estimate = -0.003 \pm 0.002$ ) (Figure 4B).

When we only considered days in which the distances moved were greater than zero (i.e., excluding days without apparent movements and the 7 individuals that did not move during the study), the mean ( $\pm SE$ ) distance moved by amphisbaenians was of  $105 \pm 15$  cm (range = 11–346 cm,  $n = 34$  individuals) (Figure 3C). This distance was significantly longer in males ( $149 \pm 26$  cm, range = 13–346 cm,  $n = 17$ ) than in females ( $61 \pm 9$  cm, range = 11–125 cm,  $n = 17$ ), and there was no overall significant effect of body size, but

the interaction was significant (Table 4). Separated GLMs showed that when smaller males actually made some movements, they moved shorter distances than larger ones (GLM:  $\chi^2 = 37.17$ ,  $P < 0.0001$ ,  $Estimate = 0.007 \pm 0.001$ ), while the opposite relationship was observed in females (GLM:  $\chi^2 = 65.48$ ,  $P < 0.0001$ ,  $Estimate = -0.012 \pm 0.002$ ) (Figure 4C).

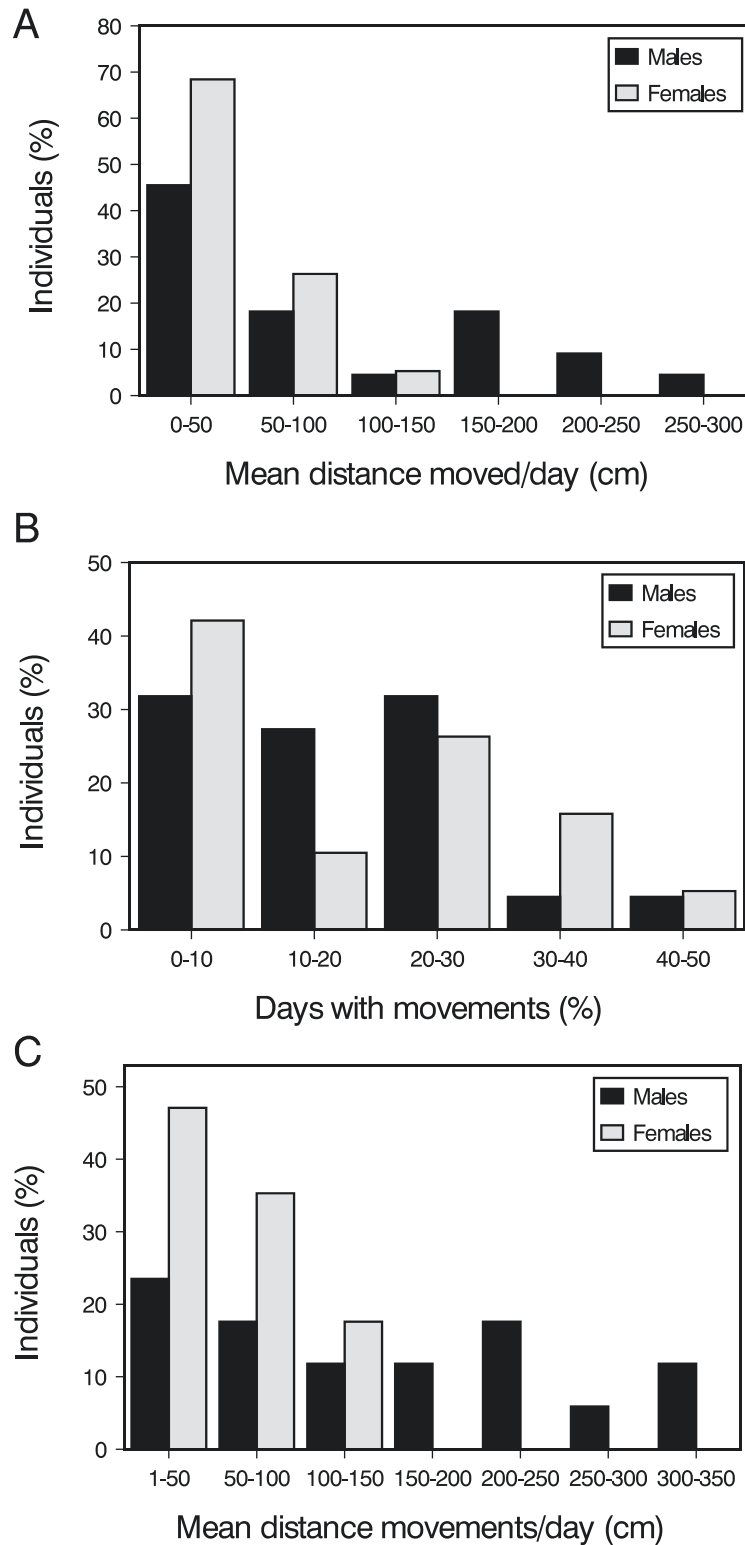
Considering the microhabitat used by the individuals that we followed using PIT-tag telemetry, only a few locations were linked to rocks (percentage of locations across individuals, mean  $\pm SE = 6.9 \pm 2.5\%$ ), followed by locations in open areas ( $35.6 \pm 6.7\%$ ) and most locations were made under the cover of *Salsola* bushes ( $57.50 \pm 6.6\%$ ). A comparison with the cover availability of these three types of microhabitats in the study plot estimated from an aerial photograph (rocks = 19%; open = 58%; bushes = 23%), showed that locations of amphisbaenians were not random ( $\chi^2 = 25.14$ ,  $P = 0.0001$ ). Interestingly, most observations linked to bushes were of animals that had not moved since the last location; 77 relocations where the individual had not moved from a total of 91 observations in bushes (84.6%), against 24 from 44 in open areas (54.5%) and 8 from 17 under rocks (47.0%) ( $\chi^2 = 18.95$ ,  $P = 0.0001$ ).

When comparing the habitats used between sexes, males were located significantly less often than females under bush cover (Mann–Whitney  $U$  test:  $U = 98.0$ ,  $Z = -2.90$ ,  $P = 0.0037$ ), but significantly more often than females in open areas ( $U = 119.5$ ,  $Z = 2.34$ ,  $P = 0.019$ ), and did not differ in the use of rocks ( $U = 166.0$ ,  $Z = 1.12$ ,  $P = 0.26$ ) (Figure 5). The body size of individuals did not significantly affect their percentage use of locations in any of these microhabitats (Spearman rank order correlations; bushes:  $r_s = -0.27$ ,  $P = 0.09$ ; rocks:  $r_s = 0.04$ ,  $P = 0.78$ ; open:  $r_s = 0.26$ ,  $P = 0.10$ ), neither when considering the sexes separately (males:  $-0.17 < r_s < 0.15$ ,  $0.43 < P < 0.66$ ; females:  $-0.23 < r_s < 0.29$ ,  $0.35 < P < 0.22$ ).

### Discussion

During the summer drought period in the Chafarías Islands (NW Africa), the amphisbaenian *T. wiegmanni* did not use the microhabitats randomly. Amphisbaenians were particularly selected when compared with their availability, sites with high abundance of medium-sized rocks, and areas under a high cover of *Salsola* bushes. We also found that the activity of *T. wiegmanni* individuals (the number of days with movements) decreased largely in summer, in comparison to a season (early spring) with optimal environmental conditions (i.e., the average proportion of days with active movements of an individual: 19% in summer vs. 65% in spring; see Martín et al. 2021). However, the amphisbaenians were not entirely inactive, made some relatively long underground movements, and used areas under bushes with better environmental conditions, but where they would have not been detected if we had not used PIT-tag telemetry.

The basic pattern of microhabitat selection and movements of *T. wiegmanni* observed in this study were similar to those found in previous studies made in spring, when weather conditions were optimal for this species (Civantos et al. 2003; Martín, López, et al. 2013, 2021). However, there were some changes in these patterns that seem to be clearly a response to the hot and dry extreme conditions of the summer in this arid region. In this regard, *T. wiegmanni* decreased its presence under rocks in summer, as the



**Figure 3.** Underground movements of undisturbed *Trogonophis wiegmanni* amphisbaenians. Frequency distribution of individuals (% within each sex;  $n = 22$  males, black, and 19 females, gray) in each category of (A) mean distance moved per day (cm), (B) percentage of days in which some meaningful movements occurred and (C) mean distance of the movements (cm) made in days when amphisbaenians actually moved (i.e., excluding days without apparent movements and 7 individuals that did not move during the study).

temperatures below them may be too high, over the preferred range of body temperatures selected by this species in a thermal gradient (21.7–23.4 °C; Gatten and McClung 1981). These changes are similar to the daily changes observed in the patterns of rock use by *T. wiegmanni* and

other amphisbaenian species in spring (López et al. 1998, 2002). Thus, within the same day in spring, individuals are found more often under rocks at times of the day when substrate temperatures allowed individuals to maintain their preferred body temperatures for longer, but less often



**Table 4.** Underground movements made by the amphisbaenian *Trogonophis wiegmanni*

	Distance moved per day		Days with movements		Distance of movements per day	
	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>
Sex	442.36	<0.0001	0.86	0.35	651.48	<0.0001
Body size	64.39	<0.0001	23.18	<0.0001	0.04	0.84
Sex × size	26.75	<0.0001	15.23	<0.0001	102.61	<0.0001

Results of GLMs testing the effects of sex, body size and its interaction on (a) mean distance moved per day, (b) percentage of days in which some meaningful movements occurred and (c) mean distance of the movements made in days when amphisbaenians actually moved (i.e., excluding days without apparent movements and seven individuals that did not move during the study). Significant probabilities are marked in bold.

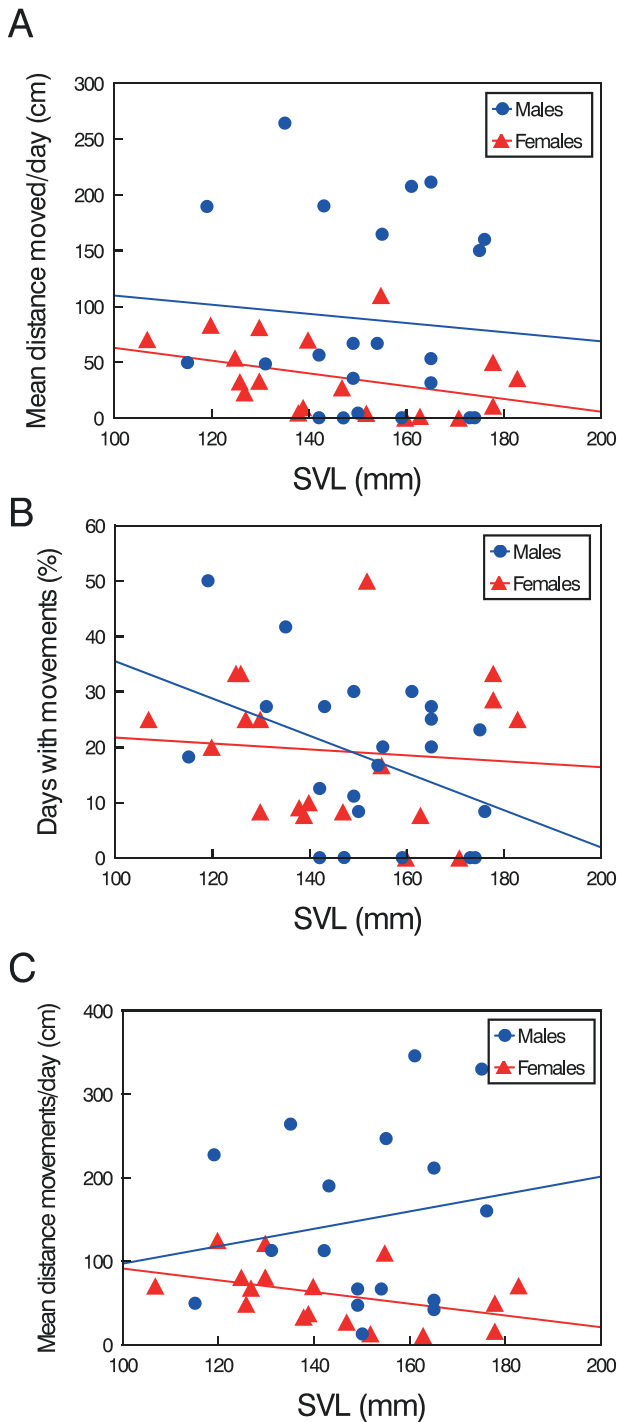
at other times when substrate temperatures were too high (López et al. 1998, 2002). By using this daily and seasonal behavioral thermoregulation, amphisbaenians would maximize fitness and performance, as other reptiles do (Angilletta 2009), and likely would also avoid body water loss derived of high temperatures to maintain their water balance (e.g., Dupoué et al. 2015). In addition, rocks are often used by *T. wiegmanni* for foraging as many of their invertebrate prey are more abundant under rocks than in other microhabitats (Martín, Ortega, et al. 2013). However, during the drought period, the availability and diversity of prey decrease in all microhabitats, but especially under rocks is much lower and many rocks are “empty” of suitable potential prey (Martín et al. 2023). Thus, rocks would not be especially attractive “hot spots” for amphisbaenians as the foraging opportunities under rocks largely decrease, while other microhabitats with better conditions (i.e., under bushes) might still hold more invertebrates.

As explained above, both, thermoregulation, water balance, and foraging requirements might force amphisbaenians in summer to either move to other sites or to decrease activity and estivate buried deep in the soil. Our data confirm that while in spring many individuals were usually found under rocks (Martín et al. 2011b, Martín, López, et al., 2013, 2021), in summer individuals were not so abundant under rocks but were more often located buried under the cover of bushes. In summer, thermoregulatory and water balance opportunities might be more favorable (i.e., lower soil temperatures and higher soil humidity) under the shadow of bushes than in open areas or under rocks exposed to the sun (e.g., Shen et al. 2022). Also, for similar thermal and humidity requirements, soil invertebrates might be more abundant under bushes in summer if humidity is higher under bushes (Staley et al. 2007; Manu et al. 2022). Future studies should examine with more detail whether seasonal changes in both temperature and humidity soil conditions and in prey availability in different microhabitats are correlated with seasonal changes in space use of amphisbaenians. Nevertheless, considering the repeated locations of the same individuals followed using PIT-tag telemetry indicated that open areas are also used frequently (although less than expected by their availability), in spite that these open areas would be exposed to unfavorable conditions. These locations, however, might be of individuals that were actively moving underground between or looking for favorable sites (i.e., bushes), where they will later stay apparently motionless for longer periods.

The surveys made using PIT-tag telemetry to follow the underground movements of *T. wiegmanni* in summer showed

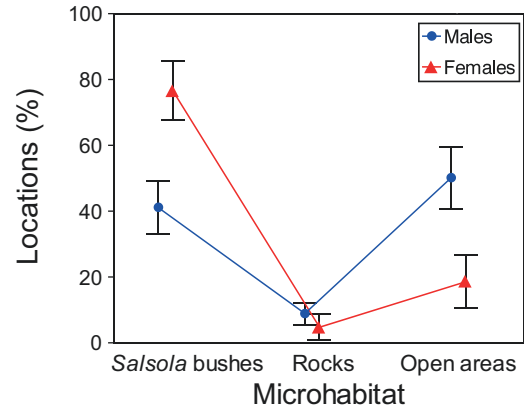
that activity of these animals decreased largely in comparison with the results of our surveys made in spring in the same study area following the same protocols (Martín et al. 2021). However, amphisbaenians did not interrupt activity entirely in summer. This suggests that a long continuous aestivation period probably did not occur, at least in most of the individuals detected and followed in this study. The changes in microhabitat use (i.e., a higher use of areas under bushes) may allow *T. wiegmanni* to find more appropriate environmental conditions and food, which would allow for maintaining activity for longer. This would be important, for example, for being able to actively move and avoid episodes of extreme heat and drought or active predators, which otherwise might be unavoidable by sleeping estivated amphisbaenians. However, there were intersexual and body size/age-related differences in movement strategies, with males moving more often and at greater distances than females, a difference that was also found during the mating season (spring) attributed to different reproductive requirements of males and females (Martín et al. 2021). In summer, the mating season has ended but reproduction is viviparous in *T. wiegmanni*, and females are pregnant throughout this season. Viviparity eliminates the need for a buffer against unpredictable periods of drought because maternal physiology protects against desiccation (Bonnet et al. 2017), but it requires that females are able to regulate behaviorally their thermal and hydric physiology as long as possible. Thus, females might reduce movements, spending long periods in favorable areas, to save energy and water and to maintain stable temperature conditions that maximize the embryo’s development (Shine 2004; López-Alcaide et al. 2017). However, males, especially younger ones, might move more while dispersing through unfavorable open areas, while looking for prey and new territories where to settle. Older males would be more territorial, showing higher long-term site fidelity (Martín et al. 2021) and moving less frequently than younger ones, but when moving older/larger males could do longer displacements.

From a methodological point of view, our study revealed that the type of survey technique may induce some bias on the apparent pattern of habitat selection (and maybe in other type of studies too). In many studies of fossorial and semi-fossorial lizards and snakes, the animals examined are only those found under rocks or other objects, even artificially provided by the researchers (e.g., Sutton et al. 1999; Kuhn et al. 2005). However, PIT-tag telemetry indicates that activity and underground movements of fossorial *T. wiegmanni* amphisbaenians also occur well away from rocky areas. Thus, when we analyzed habitat selection with data restricted to



**Figure 4.** Effects of body size on underground movements in the amphisbaenian *Trogonophis wiegmanni*. Relationships between body size (SVL) of males (blue) and females (red) and (A) mean distance moved per day (cm), (B) percentage of days in which some meaningful movements occurred and (C) mean distance of the movements (cm) made in days when amphisbaenians actually moved (i.e., excluding days without apparent movements and seven individuals that did not move during the study).

rock observations, we found some differences with respect to the telemetry data that considered all the available surfaces (i.e., rock-restricted surveys underestimated the use of bushes and grassy areas). Moreover, repeated relocations with PIT-tag telemetry of the same individuals may also show a



**Figure 5.** Microhabitat use by the amphisbaenian *Trogonophis wiegmanni*. Mean ( $\pm$  SE) percentage of locations of a given individual in each microhabitat during repeated surveys using PIT-tag telemetry.

better picture of habitat use (e.g., high use of bushes where they remained relatively motionless, but with occasional long displacements through open areas between bushy areas). Therefore, although rock or board cover surveys are a useful and easy way to find and study fossorial reptiles, the addition of other technological methodologies, such as PIT-tag telemetry, may provide new interesting insights into the ecology and behavior of these little-known animals. On the other hand, PIT-tag telemetry may also have some bias (Kuhnz 2000; Ousterhout and Semlitsch 2014; Recio et al. 2019). For example, the soil depth at which the signal of a marked animal can be detected is limited, being lower when the size of PIT tags is smaller (Ousterhout and Semlitsch 2014). Also, if 2 marked individuals are very close to each other the signals of their PIT tags might interfere and only one, or none, signal is detected. Therefore, in areas with deep soils, species that move at greater soil depths, or when there are aggregated individuals, many animals could be undetectable and this might bias the observed habitat selection patterns.

We conclude that the amphisbaenian *T. wiegmanni* seems able to cope with the summer drought periods, which are usual in its environment, by behaviorally adjusting its use of microhabitats and movement strategies. Amphisbaenians would be tracking and selecting as much as possible the underground sites where conditions are more favorable in a given moment. However, it is not known whether they would be able to maintain these, likely costly, strategies during unfavorable periods unusually longer than the normal ones, as those predicted to occur in the future under global change expectations. Future studies should examine the actual physiological costs that drought periods might infer to these animals, in spite of their behavioral strategies to compensate them and estimate whether longer periods could result in unaffordable costs that put the survival of these animals at risk.

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## Author Contributions

- José Martín conceived and designed the study, performed field work, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Gonzalo Rodríguez-Ruiz and José Javier Cuervo conceived and designed the study, performed field work, authored or reviewed drafts of the paper, and approved the final draft.

## Data Availability

The data are available at figshare: Martín, José; Rodríguez-Ruiz, Gonzalo; Cuervo, José Javier (2023): Microhabitat selection and underground movements of amphisbaenians under summer drought conditions. Dataset. Figshare. <https://doi.org/10.6084/m9.figshare.22713415.v1>.

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