

Coping with drought? Effects of extended drought conditions on soil invertebrate prey and diet selection by a fossorial amphisbaenian reptile

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Handling editor: Zhi-Yun Jia

Abstract

Arid climates are characterized by a summer drought period to which animals seem adapted. However, in some years, the drought can extend for unusually longer periods. Examining the effects of these current extreme weather events on biodiversity can help to understand the effects of climate change, as models predict an increase in drought severity. Here, we examined the effects of “unusual” extended drought on soil invertebrate prey availability and on diet composition (based on fecal contents) and diet selection of a fossorial amphisbaenian, the checkerboard worm lizard *Trogonophis wiegmanni*. Weather data show interannual variations in summer drought duration. The abundance and diversity of soil invertebrates in spring were high, and similar to those found in a “normal” early autumn, after some rain had ended with the summer drought. In contrast, in years with “unusual” extended drought, abundance, and diversity of soil invertebrates in early autumn were very low. Also, there were seasonal changes in amphisbaenians’ diet; in autumn with drought, prey diversity, and niche breadth decreased with respect to spring and autumns after some rain had fallen. Amphisbaenians did not eat prey at random in any season, but made some changes in prey selection that may result from drought-related restrictions in prey availability. Finally, in spite that amphisbaenians showed some feeding flexibility, their body condition was lower in autumn than in spring, and much lower in autumn with drought. If extended drought became the norm in the future, amphisbaenians might suffer important negative effects for their health state.

Key words: amphisbaenians, drought, feeding ecology, soil invertebrates, *Trogonophis wiegmanni*, weather conditions.

The typical climate in an arid or semiarid region is characterized by high temperatures and low precipitations, and particularly by including a more or less extensive period of dryness conditions (Trewartha and Horn 1980). In this context, many Mediterranean areas experience a typically dry and hot summer that is ended by the occurrence of some, often stormy, rain episodes that lead to the autumn and mild, wet winter (Lionello 2012). Many plants and animals are adapted to these “usual” summer drought conditions and are able to badly survive waiting for the new rains at the end of summer or early autumn, when life seems to flourish again. For example, whereas many plants remain in a quiescent mode during summer and re-grow after these rains (Dallman 1998), some animals can move temporally to better locations and come back when rain falls (Abraham et al. 2019). Other sedentary animals, such as some reptiles, are able to estivate in retreats until conditions are more favorable (Secor and Lignot 2010). However, in some years, the drought episodes can be extreme and extend for unusually longer periods, putting biodiversity in serious problems. In addition to thermal and hydric stress (Diele-Viegas and Duarte Rocha 2018), vertebrate animals

may also suffer very strong dietary restrictions related to the potential negative effects of drought on the availability of plants and animal prey (i.e., the abundance, diversity, and quality of food may decrease), increasing energetic stress and mortality (Sperry and Weatherhead 2008; Folks et al. 2014).

Moreover, within a global change context, climate models predict that the frequency and severity of drought periods will increase progressively worldwide, particularly in already arid regions (Collins et al. 2013; Hartmann et al. 2013). Examining the effects of current extreme weather events on biodiversity can be particularly useful to understand the potential effects of climate change (e.g., Westphal et al. 2016). Therefore, it is important to know the effects of the, at the moment, “unusual” longer drought periods on plants and animals, and whether these have physiological or behavioral mechanisms to cope with extreme long droughts.

Fossorial animals that spent all their life underground and have very limited dispersal abilities (Martín et al. 2021) may be particularly affected by extensive drought periods. Amphisbaenians are one notorious, but little conspicuous and understudied, group of strictly fossorial squamate reptiles (Gans 1978, 2005).

Received 29 May 2022; accepted 15 July 2022

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The most of amphisbaenian species inhabit tropical to temperate climates, and only a few species are found in more arid regions (Gans 2005). Among the latter, the checkerboard worm lizard *Trogonophis wiegmanni* inhabits Mediterranean arid regions in North Western African (Bons and Geniez 1996). In contrast to the most amphisbaenians, reproduction of this species is viviparous and females give birth to live offspring at the end of summer (Bons and Saint Girons 1963; Martín et al. 2011b). Births occur after the end of the dry summer period, which amphisbaenians often spent estivating buried at great depth to avoid extreme hot temperatures and drought (Bons and Saint Girons 1963). Therefore, for amphisbaenians “emerging” at the end of summer, and for their new born offspring, it might be extremely important that the drought period has already finished after some rain have fallen and the optimal conditions return.

The diet of the most amphisbaenians seems to be a generalist one, as they seem to feed on the most common available soil prey, such as ants or termites (e.g., White et al. 1992; Colli and Zamboni 1999; Kearney 2003; Bernardo-Silva et al. 2006; Gomes et al. 2009; Balestrin and Cappellari 2011). However, the narrow dietary spectrum of some species (mostly limited to specific small-sized arthropods) suggests a more selective foraging system (López et al. 1991; Cruz-Neto and Abe 1993; Webb et al. 2000; Vega 2001; Bernardo-Silva et al. 2006). For example, a previous study of *T. wiegmanni* amphisbaenians showed that, at least under the spring optimal weather conditions, this amphisbaenian selects some prey types (insect larvae and snails), whereas others (ants and isopods) are consumed much less than expected, almost avoided, in spite of their high abundance in the soil and under rocks (Martín et al. 2013b). However, under drought conditions, the availability of soil invertebrates is expected to be much lower in abundance and probably would have a very different and restricted taxonomic composition. Therefore, the question that arises is whether, in response to these climatic changes, amphisbaenians are still able to maintain their “optimal” diet selection patterns, or whether they are forced, or able, to change their diet to cope with severe drought restrictions.

Here, we examined the possible negative effects of “unusual” extended drought periods on the soil invertebrate prey availability and whether these lead to changes in the diet composition and diet selection patterns of *T. wiegmanni* amphisbaenians. We compared across 4 years the seasonal variation (spring vs. early autumn) in availability of invertebrates in the habitat and in the diet of amphisbaenians (based on fecal contents). We examined the relationships between diet selection patterns and interannual variations in weather conditions (i.e., “usual,” with rain at the end of summer vs. extended duration of the summer drought periods). We expected that 1) the extended drought periods will negatively affect to the soil invertebrates, decreasing the abundance and diversity of available prey, which might have negative consequences for the optimal diet of amphisbaenians, decreasing their body condition. However, 2) amphisbaenians, instead of suffering food intake restrictions, might be able to modify their diet selection patterns in response to changes in prey availability.

Materials and Methods

Study area and climatic data

We made the study at the Chafarinas archipelago (Spain) (35°11'N, 02°25'W), located in the Mediterranean Sea. These are three very small islands, Congreso (25.6 ha),

Isabel II (15.6 ha, the only one inhabited by a small human population), and Rey Francisco (13.9 ha), located 2.5 nautical miles off the northern Moroccan coast (Ras el Ma). We visited the study area during 8 campaigns of 2 weeks' duration each in spring (end of March and beginning of April) and autumn (end of September and beginning of October) from 2014 to 2017. Natural vegetation consists of small bushes adapted to salinity and drought (genera *Suaeda*, *Salsola*, *Lycium*, and *Atriplex*) (Martín et al. 2011a, 2013a).

Climatic data (temperatures and precipitations) were obtained from the daily records of the last 22 years (2000–2021) of the nearest meteorological station of “Melilla” (47 km from the study area; 35°17'26"N; 02°56'49"W) (data available from the Spanish Meteorological Agency, “Agencia Española de Meteorología, AEMET”; <http://www.aemet.es>). This station is located in the coast and experience the same climatic conditions that the study area. These data show that climate in this area is Mediterranean, dry, and warm (see Results for details).

Availability of soil invertebrates in the habitat

In each field campaign, we estimated availability of potential prey in the same areas and soil microhabitats where we captured amphisbaenians (see below). We randomly lifted rocks that might hold amphisbaenians (i.e., rocks > 10 cm length), and counted and identified for 2 min the invertebrates (restricted to those >2 mm long, as smaller ones have not been found in previous studies of the diet of this amphisbaenian; Martín et al. 2013b) according to order or, in some cases, family level that were observed on the undersurface of the turned rock and on the substrate exposed on turning. We included those invertebrates that escaped when the rock was lifted, such as isopods, spiders, or centipedes (for similar procedures, see Martín and Salvador 1993; Goldsbrough et al. 2003; Martín et al. 2013b), which would not be recorded if we merely collected soil samples for counting prey in the laboratory. Simultaneously, we gently excavated with a small stick to a depth of 5 cm in the typically loose dry sandy soil and leaf litter under the rock to look for buried invertebrates, such as insect larvae. Using this procedure, we did not intend to estimate the absolute abundance of invertebrates, but this standardized procedure allowed to estimate relative abundances of the types of invertebrates actually available for amphisbaenians in their underground microhabitats.

Amphisbaenians sampling procedures

We haphazardly followed different routes covering all the available habitats, during the day, searching for amphisbaenians by lifting rocks. Amphisbaenians were abundant and easy to find fully active under rocks, which are used for thermoregulation and foraging (López et al. 2002; Martín et al. 2011a, 2011b, 2013a, 2013b). We captured amphisbaenians by hand. Diet samples were obtained by collecting the feces of live amphisbaenians in the field. Amphisbaenians usually excreted the most gastrointestinal contents when handled, but we also gently compressed their vents to force the complete expulsion of feces. We used labeled Eppendorf vials to individually store the feces. We ensured that the same individuals were not sampled twice because amphisbaenians were marked individually with PIT-tags as a part of a long-term population study (Recio et al. 2019). Amphisbaenians were measured (see below) and later released in a few minutes at their exact point of capture after ensuring they were in good health.

Analyses of fecal contents of amphisbaenians

We identified in the laboratory the prey remains found in fecal pellets according to order or family level, using a binocular dissecting microscope. Each individual pellet was spread in a thin layer of less than 0.5 mm over the entire surface of a Petri dish with some drops of 70 °C ethylic alcohol. We made a conservative estimation of prey numbers for each fecal pellet by counting only easily identified remains. The analysis of fecal pellet contents is a standard method to quantify diet without compromising animal welfare (e.g., Angelici et al. 1997; Suarez et al. 2000; Luiselli 2006; Hawlena and Pérez-Mellado 2009; Pérez-Cembranos et al. 2016). However, to minimize the destroyer effect of digestion on small and soft-bodied prey (Pincheira-Donoso 2008), we carefully searched for body parts that are less likely to be digested, such as head capsules of insect larvae and chelicerae and fragments of cephalic region of spiders. In lizards, the comparison of diet analyses based on meticulous fecal pellet analysis or gastric contents from dead animals has shown very similar results, including proportions of soft-bodied prey (Pérez-Mellado et al. 2011).

Analyses of invertebrate's availability and amphisbaenians' diet

We characterized the availability in the habitat of each class of invertebrates using its “abundance” (total number) and “presence” (percentage of rocks containing a particular type of organism). Similarly, diet composition of amphisbaenians was characterized using the “prey abundance” (i.e., the percentage of a given prey type relative to the total prey number) and the “prey presence” (i.e., the percentage of individual amphisbaenians consuming a given prey type).

To compare the availability of prey and the diet of amphisbaenians among seasons and years, we first examined weather conditions in the 4 years of the study (see results). Then, based on these results, we pooled data of availability or diet for the “spring” surveys of the 4 years, and divided autumn data in 2 categories, namely, “autumn with drought” (pooled data of years 2015 and 2016) or “autumn after rain” (years 2014 and 2017). The interseasonal variations in availability or diet, and the relationships between availability and diet were compared using χ^2 tests.

Diversity of invertebrates in the habitat and in the diet (excluding unidentified remains) were calculated by means of the Shannon–Weaver index ($H' = -\sum p_i \ln p_i$) for the taxonomic categories identified (Magurran 1988). To compare H' indexes between seasons, we used the Hutcheson t -test (Hutcheson 1970). We estimated the diet breadth of amphisbaenians using the $DB(\chi^2)$ index proposed by Saikia (2012), computed as $DB(\chi^2) = \sum (\log O_i - \log E_i)^2 / \log E_i$, which considers both observed values of food items (O) and available food resources as expected values (E). To estimate the overlap in diet composition of amphisbaenians between seasons, we used the symmetric index of Pianka (1973) [$O_{jk} = (\sum p_{ij} p_{ik}) / \sqrt{(\sum p_{ij}^2)(\sum p_{ik}^2)}$], where p_{ij} is the relative occurrence of taxon i in the diet in the season j and p_{ik} is the relative occurrence of taxon i in the diet in the season k . The index is scaled from 0 to 1, with 1 indicating complete overlap.

To estimate selection for a prey type, we used the selectivity index (D) of Ivlev (1961) modified by Jacobs (1974): $D = (r - p) / (r + p - 2rp)$, where r is the proportion of a given prey type in amphisbaenians diet and p is its proportion available in the environment. We selected this index because it is widely

used in the most studies of trophic preferences. This selectivity index ranges from -1 (total avoidance) through 0 (no or random selection) to $+1$ (maximum positive selection). To test the significance of the electivity index of a prey type, we used χ^2 tests comparing observed proportions of the number of each prey type in feces in relation to the numbers of all other prey types in feces, with expected proportions based on similar data from prey available in the habitat (restricted to groups actually consumed). Statistical analyses were made with the Statistica 8.0 software (StatSoft Inc., Tulsa, OK) or with our own custom made Excel sheets.

Body condition of amphisbaenians

To characterize body size of amphisbaenians, we measured with a metallic ruler (to the nearest 1 mm) the snout-to-vent length (SVL; from the tip of the snout to the extreme posterior point of the cloacal flap; mean \pm standard error (SE) = 134 ± 1 mm) and tail length (mean \pm SE = 10 ± 1 mm). We used a portable digital balance to measure body mass to the nearest 0.01 g (mean \pm SE = 3.55 ± 0.06 g). Due to logistic problems, not all individual sampled could be measured. We calculated as a body condition index (BCI) the residuals of an ordinary least squares linear regression of log-transformed mass against log-transformed total length (i.e., SVL + tail length) ($R^2 = 0.79$, $F_{1,1129} = 4,238.10$, $P < 0.0001$). These residuals are usually considered as the cleanest way to separate the effects of condition from the effects of body size (Bonnet and Naulleau 1994; Jakob et al. 1996; see reviews in Green 2001; Schulte-Hostedde et al. 2005). BCIs are used as proxies of health state in reptiles and many other animals (Wikelski and Cooke 2006; Amo et al. 2007; Brischoux et al. 2012).

We used general lineal models (GLMs) to test for differences in BCIs (dependent variable) between seasons and years (fixed factors), and included the interaction in the model to test whether the potential differences between seasons depended on the occurrence of rains prior to autumn. We ensured that the test met the assumptions of normality and homogeneity of variances. Post-hoc pairwise comparisons were made using Tukey's tests.

Results

Climate and weather variability

In the last 22 years, the climate at the Chafarinas Islands region has been characterized by long, cool, wet, windy, and partly cloudy winters and short, hot, muggy, arid, and mostly clear, summers (Figure 1A). During the course of the year, the temperature generally ranges from 10 °C to 30 °C and rarely drops below 7 °C or rises above 34 °C. Mean annual precipitations was of 382 mm. A typical drought period, with very scarce or no rain at all, typically occurs from June to September, although in the most years, but not others, rain episodes have been registered at the end of August or beginning of September (65% in the last 22 years), whereas in other years, drought was longer as rain did not fall until the end of September or beginning of October (35% in the last 22 years). During the 4 years of this study, we could identify 2015 and 2016 as years with extended summer drought periods (with no or almost negligible rain between June and until late September; 4 mm in 2015 and 7 mm in 2016), whereas 2014 and 2017 registered significant rains at the end of summer (end of August or beginning of September; 61 mm in 2014 and 40 mm in 2017) (Figures 1B and 2).

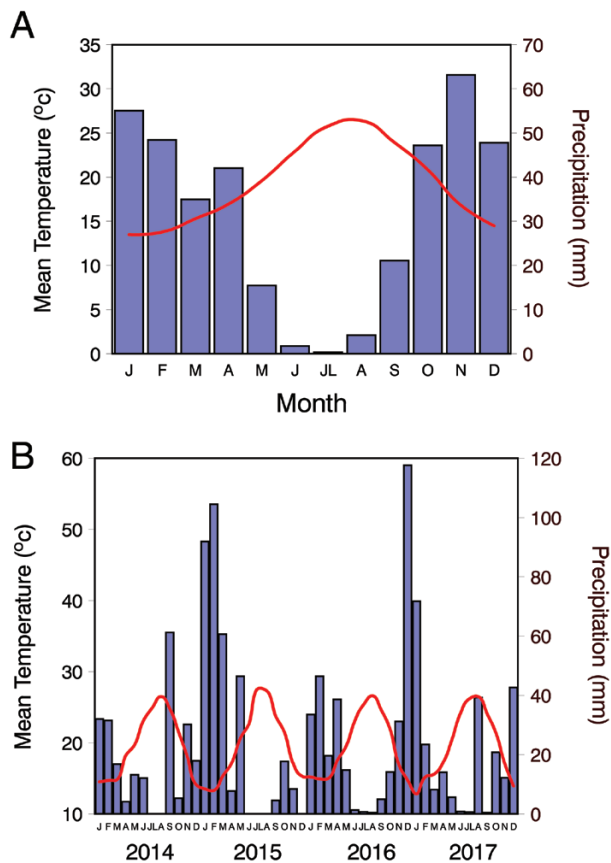


Figure 1. Climate characteristics at the Chafarinas Islands. Average monthly values of precipitation (bars) and temperature (line) (A) in the last 22 years (2000–2021) and (B) in each year during the study (2014–2017) are shown.

Availability of potential invertebrate prey

We estimated the availability of soil invertebrates under a total of 348 rocks during the 4 study years (spring = 193; autumn with drought = 80; autumn after rain = 75), of which the most rocks (89.9% overall) contained some invertebrates larger than 2 mm. The proportion of rocks empty of potential prey was similar in spring (7.2%) than in autumn after rain (10.7%) ($\chi^2 = 0.83$, $P = 0.36$), but empty rocks were significantly more abundant in autumn with drought (16.2%) than in spring ($\chi^2 = 5.14$, $P = 0.023$), although there were not significant differences between both types of autumn ($\chi^2 = 1.03$, $P = 0.31$).

The total number of invertebrates found under each rock (mean \pm SE = 11.8 ± 1.6 inv./rock, $n = 4,099$) differed significantly among seasons (GLM, $F_{2,345} = 5.03$, $P = 0.003$), being significantly lower in autumn with drought than in spring (Tukey's test, $P = 0.004$) or in autumn after rain ($P = 0.009$), whereas the abundance in spring and autumn after rain did not differ ($P = 0.93$) (Table 1). There were also seasonal differences in the relative proportions of the different types of invertebrates available under rocks (spring vs. autumn with drought: $\chi^2 = 65.60$, $df = 17$, $P < 0.0001$; spring vs. autumn after rain: $\chi^2 = 733.83$, $df = 17$, $P < 0.0001$; autumn with drought vs. autumn after rain: $\chi^2 = 39.31$, $df = 17$, $P < 0.002$) (see Table 1). Although in spring the 3 most abundant invertebrate types were in order of abundance Formicidae

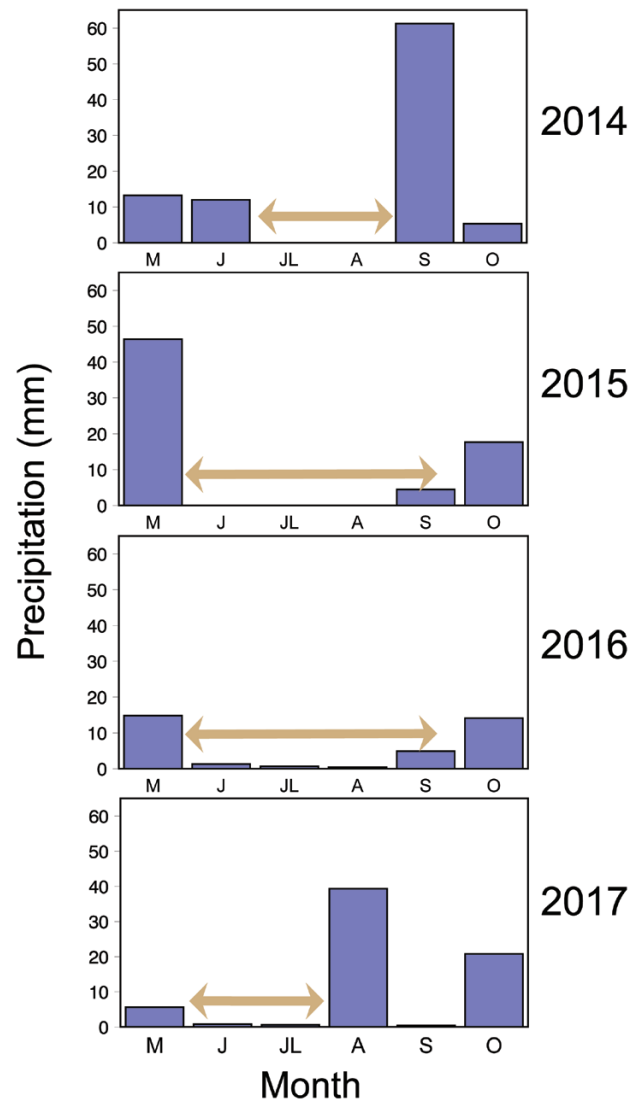


Figure 2. Summer and autumn rain and drought at the Chafarinas Islands. Average monthly values of precipitation (bars) from May to October during the study (2014–2017) and duration of the summer drought period (line with arrows) are shown.

(ants), Isopoda (isopods), and Gastropoda (snails) (these 3 groups accounting for 78.2% of all invertebrates), in autumn with drought the most abundant types were Formicidae, Gastropoda, and Coleoptera (beetles) (95.2% of all invertebrates), and in autumn after rain Formicidae, Gastropoda, and Heteroptera (bugs) (70.3% of all invertebrates). Considering the presence under rocks, the invertebrates most frequently found in spring were Gastropoda, Coleoptera, and Isopoda, whereas in autumn with drought were Coleoptera, Gastropoda, and Formicidae, and in autumn after rain were Gastropoda, Coleoptera, and Heteroptera.

Moreover, the diversity of invertebrate types in autumn with drought was significantly lower than in spring (Hutcheson t -test, $t_{1592} = 8.04$, $P < 0.0001$) and it also was lower in autumn with drought than in autumn after rain ($t_{1417} = 10.74$, $P < 0.0001$). Diversity was significantly lower in spring than in autumn after rain ($t_{1918} = 3.71$, $P = 0.0002$) (Table 1).

Diet of the amphisbaenians

We examined fecal contents from a total of 1,235 amphisbaenians during the 4 study years (spring = 555; autumn with drought = 420; autumn after rain = 260), from which 1,550 prey were recovered (prey items/fecal pellet, mean \pm SE = 1.3 ± 0.2 ; range = 1–3). The main prey components of the diet of amphisbaenians were similar between seasons. In all the seasons Insect larvae, followed by Coleoptera and Gastropoda comprised the bulk of the diet, as these were the most abundant and frequent prey types (these 3 types accounting for an overall 77.5% of prey), with other invertebrates being found in lower proportions (Table 2). Thus, there was a very high niche overlap in the diet between seasons (spring vs. autumn with drought: $O = 0.94$; spring vs. autumn after rain: $O = 0.92$; autumn with drought vs. autumn after rain: $O = 0.97$). However, there were some significant differences between seasons in the relative contribution of the different prey types to the diet, such that diet composition differed significantly between spring and autumn (spring vs. autumn with drought: $\chi^2 = 32.46$, $df = 14$, $P = 0.003$; spring vs. autumn after rain: $\chi^2 = 58.18$, $df = 14$, $P < 0.0001$), but there were not significant differences between the 2 types of autumn (autumn with drought vs. autumn after rain: $\chi^2 = 18.99$, $df = 17$, $P = 0.16$) (see Table 2).

Moreover, the diversity of invertebrate prey types (excluding unidentified remains) in the diet of amphisbaenians in spring was significantly higher than in autumn with drought (Hutcheson t -test, $t_{884} = 2.88$, $P = 0.004$) (Table 2), but diversity did not differ between spring and autumn after some rain fell at the end of summer ($t_{469} = 0.03$, $P = 0.98$). Diversity in autumn was significantly higher after rain than in a drought period ($t_{616} = 2.15$, $P = 0.032$) (Table 2). Similarly, diet breadth of amphisbaenians (excluding unidentified remains) was clearly much higher in spring than in autumn with drought, and was also higher in spring than in autumn after rain, but with a lower magnitude (Table 2). Also, diet breadth in autumn was higher after rain than in a drought period (Table 2).

Diet selection patterns

The relative proportion of the different types of invertebrates in the amphisbaenians diet did not significantly reflect the availability of these invertebrates in the habitat in any season (available vs. diet, spring: $\chi^2 = 5,050.09$, $df = 17$, $P < 0.0001$; autumn with drought, $\chi^2 = 3,392.47$, $df = 17$, $P < 0.0001$; autumn after rain, $\chi^2 = 1533.06$, $df = 17$, $P < 0.0001$). Particularly, some available invertebrate types such as Acarina, Thysanura, Embioptera, or Diptera were not consumed in any season (Table 3). Instead, amphisbaenians in spring selected positively and significantly prey such as Insect larvae, Coleoptera, and Gastropoda (Table 3), whereas prey types such as Formicidae, Chilopoda, and Isopoda were consumed in significantly lower proportions to their availability. However, this pattern of selection slightly changed in autumn; in autumn after rain, amphisbaenians selected Insect larvae, but also Isopoda, and avoided Formicidae, Heteroptera, and Gastropoda, whereas in autumn with drought, amphisbaenians selected Insect larvae, but also other groups such as Araneae or Dictyoptera, and avoided Formicidae and Gastropoda (Table 3).

Diversity of prey in the diet of amphisbaenians (Table 2) did not significantly differ of diversity of invertebrates

available in the habitat (Table 1) in spring (Hutcheson t -test, $t_{1476} = 0.06$, $P = 0.95$). However, diversity in the diet was significantly lower than in the habitat in autumn after rain ($t_{423} = 2.06$, $P = 0.04$), whereas in autumn with drought, diversity in the diet was significantly higher than in the habitat ($t_{851} = 2.65$, $P = 0.008$) (Tables 1 and 2).

Body condition of the amphisbaenians

Body condition of amphisbaenians varied significantly between seasons, being greater in spring than in summer (GLM, $F_{1,1123} = 448.51$, $P < 0.0001$) and also varied significantly between years ($F_{3,1123} = 158.09$, $P < 0.0001$), but the interaction was significant ($F_{3,1123} = 45.66$, $p < 0.0001$) (Figure 3). Thus, in all years, body condition was significantly greater in spring than in summer (Tukey's tests, $P < 0.001$ for all years), but the magnitude of such seasonal differences varied depending of the year; in years with extended drought, average body condition in autumn was negative, whereas in years when autumn occurred after rain, body condition was positive.

Discussion

Our study shows that the typical summer drought period of the Mediterranean semi-arid climates of North Africa, which usually ends when rain falls at the end of summer (Lionello 2012), leads to an autumn with conditions similar to those of spring and apparently favorable for soil invertebrates and their fossorial predator amphisbaenians. However, meteorological data of our study area show that in some years this drought period can have an unusual longer duration, maintaining the unfavorable conditions for longer in a season that might be critical for amphisbaenians, as births are taking place in early autumn and amphisbaenians have to recover from the summer estivation period (Bons and Saint Girons 1963).

Our surveys under rocks show that the abundance and diversity of soil invertebrates in spring are high, coinciding with the most favorable weather conditions of the year in this area. In a "normal" early autumn, after some rain has ended with the summer drought, abundance of soil invertebrates seems similar to those of spring and diversity is even higher, although taxonomic composition is somewhat different. In contrast, in some years with "unusual" extended drought periods, the unfavorable summer conditions remain for longer, and in early autumn abundance and diversity of soil invertebrates available under rocks are still very low. Other studies, also in other habitats and under different climatic conditions, had already shown experimentally that drought causes a decline in soil microarthropod abundances and reduces soil invertebrate feeding activity (e.g., Lindberg et al. 2002; Blankinship et al. 2011; Flórián et al. 2019; Siebert et al. 2019).

There were some seasonal changes in the diet of *T. wiegmanni* amphisbaenians which probably could be related to the different availability of invertebrates due to the different weather conditions in different seasons. Interestingly, although not surprisingly, under extended drought conditions, amphisbaenians might seem still able to find enough prey, but the diversity of prey and diet breadth decreased significantly with respect to spring and to autumns after some rain had fallen. These expected negative effects of drought are observed in the diet of other animals. For example, seasonal changes in the

Table 1. Seasonal variation in relative abundance of invertebrates (>2 mm) under rocks at the Chafarinas Islands

Invertebrates	Spring			Autumn (withdrought)			Autumn (after rain)		
	(n = 193 rocks)			(n = 80 rocks)			(n = 75 rocks)		
	Abundance		Presence	Abundance		Presence	Abundance		Presence
	n	%	%	n	%	%	n	%	%
Gastropoda	302	11.4	48.7	193	28.0	52.5	183	24.6	81.3
Pseudoscorpion	10	0.4	3.6	2	0.3	2.5	6	0.8	6.7
Araneae	54	2.0	21.2	7	1.0	8.8	9	1.2	10.7
Acarina	25	0.9	4.1				1	0.1	1.3
Isopoda	396	14.9	40.4	4	0.6	3.8	1	0.1	1.3
Chilopoda	56	2.1	17.6	2	0.3	2.5			
Thysanura	110	4.1	19.7	18	2.6	11.3	60	8.1	26.7
Dictyoptera	5	0.2	2.1				2	0.3	2.7
Embioptera	27	1.0	3.1				3	0.4	2.7
Homoptera	4	0.2	2.1				1	0.1	1.3
Heteroptera	14	0.5	2.6				144	19.3	29.3
Diptera	6	0.2	3.1						
Lepidoptera pupae	5	0.2	2.6						
Neuroptera larvae									
Coleoptera	258	9.7	42.0	163	23.7	53.8	138	18.5	46.7
Hymenoptera	2	0.1	1.0						
Formicidae	1376	51.9	26.9	300	43.5	20.0	196	26.3	14.7
Insect larvae	5	0.2	2.6	3	0.4	3.8	8	1.1	9.3
Total invert.	2650			689			752		
Invert. per rock (mean ± SE)	13.7 ± 2.7			8.6 ± 2.0			10.0 ± 1.2		
Diversity (H')	1.594			1.288			1.728		
$s^2 H'$	0.001			0.001			0.001		

Estimations based on 348 random habitat samples. Abundance (total number and %), presence (% rocks containing a particular organism), total number of invertebrates per rock, and diversity index (H') are given.

weather affect the diet of lizards (Lunney et al. 1989; Pérez-Cembranos et al. 2016). Also in herbivorous mammal species, diet richness, diversity, breadth, and food quality tended to be lower under drought conditions (Van Horne et al. 1998; Folks et al. 2014).

The comparisons of proportions of prey types in the diet to those available in the habitat showed that *T. wiegmanni* amphisbaenians did not eat prey at random in any season, but selected some particular prey types, whereas consistently avoided others, in spite of important seasonal changes in prey availability. Insect larvae and pupae, mainly from Coleoptera, are the main prey of this amphisbaenian (see also Martín et al. 2013b). Although the abundance of these larvae in the habitat is very low in comparison with other invertebrates, the high energy and water content provided by this prey type (Finke 2002) might compensate the costs of finding one larvae in any season. The adult beetles (Coleoptera) are also a main prey, but comparing with their abundance in the habitat, they are moderately selected in spring, but do not seem to be particularly selected in autumn.

Ants (Formicidae) are only a small part of the diet of *T. wiegmanni* amphisbaenians, which actually seem to avoid the most ants as prey, if we consider the very high abundance of ants under rocks. This contrast with other amphisbaenian species that feed mainly on ants and termites (e.g., Riley et al.

1986; Webb et al. 2000; Kearney 2003). These amphisbaenians species are generally those with gape size limitations for feeding on large prey and, which are probably constrained to feed on these small prey types (Gans 1974, 1978). Notoriously, *T. wiegmanni* amphisbaenians consistently avoid ants even under drought conditions, when ants are almost half of all available invertebrates and it could be initially expected that ants might have been considered an alternative food resource when other preferred prey types are scarce. However, some ant species may be avoided as they can defend themselves very effectively and aggressively against amphisbaenians (López and Martín 1994) and, in general, small ants may not be an energetically and nutritional optimal prey for this amphisbaenian that is able to feed on large prey.

Snails (Gasteropoda) are one of the main selected prey of *T. wiegmanni* in spring (see also Martín et al. 2013b), which is a highly unusual prey in other amphisbaenian species (but see Pregill 1984). However, in early autumn, snails accounted for a lower proportion of the diet and are apparently avoided, considering their high availability. This amphisbaenian has specialized feeding strategies to feed on snails (Baeckens et al. 2017), and although is able to crush small-sized snails, it mainly uses an alternative strategy to feed on large gastropods by entering the snail's shell via the opening (= shell aperture) and by eating the soft tissue from

Table 2. Seasonal variation in the composition of the diet of the amphisbaenian *Trogonophis wiegmanni* at the Chafarinas Islands

Prey type	Spring			Autumn (with drought)			Autumn (after rain)		
	<i>(n</i> = 555 feces)			<i>(n</i> = 420 feces)			<i>(n</i> = 260 feces)		
	Abundance		Presence	Abundance		Presence	Abundance		Presence
	<i>n</i>	%	%	<i>n</i>	%	%	<i>n</i>	%	%
Gastropoda	155	22.8	30.4	57	11.0	13.5	45	14.5	18.4
Pseudoscorpion				3	0.6	0.7			
Araneae	13	1.8	2.4	19	3.7	4.5	7	2.3	2.9
Isopoda	74	10.0	13.8	9	1.9	2.3	5	1.6	2.0
Chilopoda	2	0.4	0.5						
Dictyoptera	1	0.2	0.4	7	1.5	1.9	1	0.3	0.3
Homoptera							1	0.3	0.4
Heteroptera	5	0.9	1.2	1	0.2	0.3	23	6.7	8.0
Lepidoptera pupae	3	0.5	0.7				1	0.3	0.4
Neuroptera larvae	1	0.1	0.1						
Coleoptera	184	23.0	28.1	138	27.0	32.1	56	17.9	21.3
Hymenoptera	3	0.3	0.3	5	1.0	1.2	4	1.3	1.7
Formicidae	20	3.3	4.3	13	2.5	2.4	14	4.4	5.4
Insect larvae	219	30.9	40.3	217	41.8	50.0	131	41.3	49.5
Arthropoda indet.	38	5.9	8.1	45	8.8	10.8	30	9.0	10.8
Total prey	718			514			318		
Diversity (H')	1.597			1.434			1.595		
$s^2 H'$	0.001			0.002			0.003		
Diet breadth ($DB(\chi^2)$)	60.246			24.851			46.437		

Composition based on 1235 fecal samples collected from live amphisbaenians. Abundance (total number and %) of prey, presence (percentage of fecal samples containing a particular prey item), diversity (H'), and niche breadth (B) indexes are shown.

inside (Baeckens et al. 2017). However, in land snails of arid regions, one common strategy against drought is estivation, which includes the production of a thick epiphragm to seal the shell aperture to avoid desiccation (e.g., Arad et al. 1989; Schweizer et al. 2019). Thus, in a drought period, “closed” snails might not be actually accessible to amphisbaenians, even if they are abundantly available under rocks (where snails have retreated to avoid high temperatures and drought) (Schweizer et al. 2019). Also, it is likely that not all these closed snail shells recorded in our autumn surveys “contained” live animals, as some of them might have finally died by desiccation. This might explain the observed seasonal changes in snail importance in the diet. Therefore, if we assume that snails are a preferred prey for an optimal diet in this amphisbaenian, the drought period would probably restrict the possibility of feeding on a large number of snails.

Other changes in diet related to the drought period may be the inclusion or increase in consumption of prey types such as spiders (Araneae), cockroaches (Dictyoptera), pseudoscorpions, or small wasps (Hymenoptera), which were scarce or absent in the diet of amphisbaenians in spring. This suggests that the restrictions in abundance and diversity of available invertebrates during the drought period might force amphisbaenians to be more generalists and include prey types not normally consumed, which probably are the only suitable found under these conditions, but that would be avoided if other preferred prey types would have been available.

The direct consequences on physiology and survival of these changes, or probably restrictions, in diet of amphisbaenians due to the unfavorable weather drought conditions need to be examined in detail. However, we found that average body condition of the population of amphisbaenians was lower in autumn, after the drought period, than in spring, and much lower in autumn in years were the drought period was longer. This may suggest that changes or limitations in food intake affected body fat reserves of amphisbaenians. Similarly, in many other animals, unfavorable drought conditions often lead to low food intake and decreased body condition (e.g., Goughwin et al. 1984; Sperry and Weatherhead 2008; Buxton et al. 2018; Bucciarelli et al. 2020). This is important because a poor body condition often leads to adverse health effects such as lower immune responses that may even increase mortality (Acevedo-Whitehouse and Duffus 2009). Moreover, several studies support a link between growth rates and ecosystem productivity via climate effects (e.g., Heulin 1985; Bauwens and Verheyen 1987; Aragón and Fitze 2014). Thus, a lower food intake might also negatively affect amphisbaenian growth, as it has been shown in other Mediterranean reptile species, where lower abundance and diversity of arthropods (i.e., potential prey) in late summer, when dry conditions are present, correlate with lower lizard growth rates (Ortega et al. 2017).

Nevertheless, in addition to a lower food intake, the low soil water availability during the drought period may increase osmotic dehydration of tissues (Shoemaker and Nagy 1977),

Table 3. Seasonal variation in diet selection patterns of the amphisbaenian *Trogonophis wiegmanni* at the Chafarinas islands

	Spring		Autumn (with drought)		Autumn (after rain)	
	Electivity index		Electivity index		Electivity index	
	<i>D</i>	<i>P</i>	<i>D</i>	<i>P</i>	<i>D</i>	<i>P</i>
Gastropoda	+0.393	<0.0001	-0.517	<0.0001	-0.310	0.0001
Pseudoscorpion	-1		+0.326	0.44	-1	
Araneae	-0.055	0.005	+0.580	0.002	+0.323	0.32
Acarina	-1				-1	
Isopoda	-0.224	<0.0001	+0.538	0.055	+0.850	0.007
Chilopoda	-0.719	<0.0001	-1			
Thysanura	-1		-1		-1	
Dictyoptera	+0.107	0.32	+1	0.011	-0.039	0.96
Embioptera	-1				-1	
Homoptera	-1				+0.447	0.59
Heteroptera	+0.252	0.38	+1	0.84	-0.533	<0.0001
Diptera	-1					
Lepidoptera pupae	+0.475	0.93			+1	0.15
Neuroptera larvae						
Coleoptera	+0.469	0.028	+0.087	0.33	-0.016	0.38
Hymenoptera	+0.556	0.26	+1	0.045	+1	0.004
Formicidae	-0.940	<0.0001	-0.936	<0.0001	-0.770	<0.0001
Insect larvae	+0.992	<0.0001	+0.988	<0.0001	+0.970	<0.0001

The electivity index of Jacobs for each potential available prey type (*D*) and statistical significances (*P*, from a χ^2 test) of this index are given. Significant electivities are marked in bold.

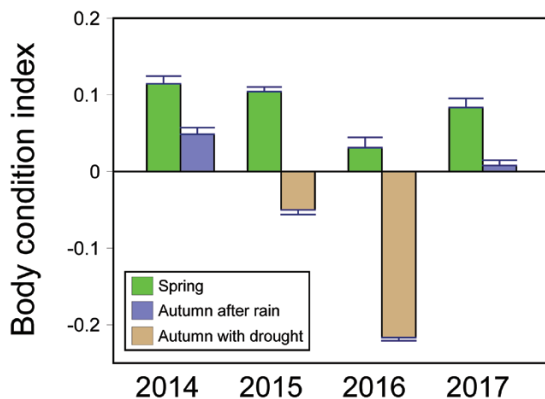


Figure 3. BCI of the amphisbaenian *Trogonophis wiegmanni* at the Chafarinas Islands. Average (\pm SE) values of body condition (i.e., residuals of a linear regression of log-transformed mass against log-transformed total length) in spring and autumn of each year during the study (2014–2017) are shown.

which will also contribute to decrease body condition of amphisbaenians. Thus, previous observations in the same study area showed that spatial differences in soil salinization, which reduced soil water availability, affected negatively to body condition of these amphisbaenians (Martín et al. 2015). In any case, increased drought weather conditions may negatively affect reproduction and, consequently, the survival of animal populations. For example, in the viviparous desert lizard *Eremias multiocellata*, low precipitation and increased drought affect negatively the gestation period and reproductive output of females (Wang et al. 2016). Moreover, female *E. multiocellata* lizards facing experimental food restrictions lay fewer offspring, although with unchanged body size,

but incur the cost of poor postpartum body condition and immune function (Wang et al. 2017). Similarly, severe declines of available prey reduced energy acquisition during drought, negatively impacting reproductive output of the pitviper snake *Agkistrodon contortrix*, a live-bearing capital breeder (Smith et al. 2019).

Our results suggest that populations of *T. wiegmanni* amphisbaenians may be at least partially able to deal with unfavorable but, at the moment, not very common extended drought weather. With respect to the diet, these amphisbaenians seem able to show some flexibility in their feeding habits to deal with restrictions in prey availability, although nonetheless diversity and probably quality of prey in the diet decreases. These changes in diet may have negative effects because when amphisbaenians suffered suboptimal dry weather in some years, leading to food restrictions, their body condition decreased. Nevertheless, because, at the moment, the extended drought periods are usually ended in a relatively short time, we suggest that the observed temporal negative consequences on body condition might not be very relevant and amphisbaenians might quickly recover when optimal environmental conditions return. In this regard, we have not observed apparent obvious variations in amphisbaenian abundance or mortality related to years with more or less rain in early autumn (personal observation). However, future studies should examine whether a lower body condition affect to the health state, reproductive output and survivorship of an individual and whether these effects may have consequences for populations survival. Moreover, the question that arises is that if these extended drought episodes became the norm in the future, as predicted by global change models, whether

amphisbaenians might be able to cope with these unfavorable conditions during longer and more frequent periods without suffering important negative effects for their health state and population survival.

Acknowledgments

We thank G Moreno-Rueda and an anonymous reviewer for helpful comments. We also thank the field station of the “Refugio Nacional de Caza de las Islas Chafarinas” for logistical support, and J.I. Montoya, J. Díaz, G. Martínez, A. Sanz, F. López, and A. Ruiz for support and friendship in the Islands. The field study and capture of amphisbaenians were approved by the Spanish “Dirección General de Calidad y Evaluación Ambiental y Medio Natural” of the “Ministerio de Agricultura, Alimentación y Medio Ambiente” (number 12706). Research procedures were approved by the “Comisión Ética de Experimentación Animal (CEEA)” of the Museo Nacional de Ciencias Naturales, CSIC.

Funding

Financial support was provided by the Spanish Ministerio de Ciencia, Innovación y Universidades project PGC2018-093592-B-I00 (MCIU/AEI/FEDER, UE).

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