2024. Journal of Arachnology 52:189–198

Foraging strategies, prey selection and size- and microhabitat-related diet variation in *Buthus montanus* (Scorpiones: Buthidae) in an arid area of SE Spain

Francisco Sánchez-Piñero[1], **Fernando Urbano-Tenorio**[1] and **Leticia Puerta-Rodríguez**[1,2]: [1]Departamento de Zoología, Facultad de Ciencias, Universidad de Granada, 18071 Granada, Spain; E-mail: fspinero@ugr.es; [2]Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, 28006 Madrid, Spain.

Abstract. Scorpions are diverse and abundant in tropical and subtropical regions worldwide, especially in arid ecosystems where they play a relevant role as predators. However, few studies have examined diet composition, use of alternative foraging strategies, prey selection, and predator-prey size relationships of scorpions in different microhabitats. This study provides an analysis of the diet of *Buthus montanus* Lourenço & Vachon, 2004 in an arid area of SE Spain. Prey captured by scorpions were recorded during black-light censuses over the main activity season of *B. montanus* in the study area. Because scorpions were observed capturing prey on the ground surface, below ground, and in vegetation, prey availability was estimated using complementary methods for shrub- and ground-dwelling prey. Results show that *B. montanus* is a generalist predator that feeds on a diverse array of prey, although predatory arthropods and tenebrionid larvae comprised the highest proportion of its diet in both number of prey and biomass. Cannibalism was a major component of its diet, accounting for almost 25% of the biomass ingested, especially in large scorpions. The composition of the diet, prey-size variability, and predator-prey size relationship showed size-related differences. These size-related variations in the diet were also linked to habitat use, due to climbing vegetation by smaller scorpions. These results highlight the implications of ontogenetic shifts in the diet of *B. montanus* related to cannibalism by larger scorpions and climbing vegetation by smaller individuals, causing changes in the type of prey used by individuals of different size and predator-prey size relationships.

Keywords: Cannibalism, ontogenetic diet shift, predator-prey size relationship, prey composition

https://doi.org/10.1636/JoA-S-23-008

Scorpions have extraordinary popular mystique as dangerous, venomous animals, provoking both fascination and fear as well as occult beliefs in disparate cultures since antiquity (Cloudsley-Thompson 1990). With more than 2700 living species (Rein 2023) distributed on all continents except Antarctica, they are especially diverse and abundant in subtropical and tropical regions, particularly in arid areas (Polis 1990). Despite their relevant ecological role as predators in arid ecosystems (Polis & McCormick 1986a; Polis & Yamashita 1991) and the prevalence of scorpionism in some regions (Chippaux & Goyffon 2008; Santos et al. 2016), there is a limited knowledge of some aspects of scorpion biology, such as feeding ecology and diet. Thus, although a number of studies report observations on their feeding behavior and prey (e.g., Casper 1985; Toscano-Gadea & Costa 2006; Miranda et al. 2015; Ojanguren-Affilastro et al. 2016; Rodríguez-Cabrera et al. 2021) or provide a qualitative description of their diet (Shachak & Brandt 1983; Castilla & Pons 2007; see also McCormick & Polis 1991 for a summary), very few works, concerning only four species (the buthids *Centruroides vittatus* (Say, 1821), *Mesobuthus eupeus* (CL Koch, 1839), *M. gibbosus* (Brullé, 1832), and the vaejovid *Smeringurus mesaensis* (Stahnke, 1957)), have quantitatively analyzed scorpion diet (Polis 1979; Yamashita 2004; McReynolds 2008, 2020, 2022; Kaltsas et al. 2008; Novruzov 2017a, b).

Apart from diet composition, other aspects of scorpion diet have been examined in very few works. Scant information is available on important topics of scorpion feeding ecology such as prey selectivity, variation of foraging behavior and diet among microhabitats, and predator-prey size relationships. Although selection of prey taxa is a feature of generalist predatory arthropods (Eubanks & Denno 2000; Symondson et al. 2002; Mukherjee & Heithaus 2013), this aspect of the diet of scorpions has seldom been analyzed. Novruzov (2017a) studied prey selection by *Mesobuthus eupeus* and found weak (positive and negative) selectivity values for most prey, except for a few unselected taxa (lizards, Mantodea, Odonata).

Ontogenetic dietary shifts are also common in predators with size-structured populations (Polis 1984; Sánchez-Hernández et al. 2019; Suzuki et al. 2022). Polis (1979, 1984), Polis & McCormick (1986b), and McReynolds (2020) analyzed age/size differences in the diet of *C. vittatus, S. mesaensis*, and other desert scorpion species, revealing marked dietary differences among age classes. Ontogenetic differences in the diet of predators have also been found to be related to changes in predator-prey size relationships (Cohen et al. 1993; Nakazawa et al. 2011, 2013), but evidence for such relationships is limited for scorpions. Polis (1984) analyzed the predator-prey size relationship in *S. mesaensis*, indicating that larger scorpions not only consume prey that are on average larger, but also span a larger variance in size. Kaltsas et al. (2008) reported a linear or positive curvilinear relationship between scorpion size and prey size in *Mesobuthus gibbosus* in the Aegean archipelago, concluding that prey selection differed between juvenile and mature individuals.

Size- and age-related shifts in foraging behavior and (micro)habitat use have been shown to cause changes in the diet of diverse predatory taxa (Werner & Gilliam 1984; Dahlgren & Eggleston 2000; Griffiths 2020). However, diet variation due to alternative foraging strategies used by scorpions in contrasting microhabitats during different developmental stages has received little attention. McReynolds (2008, 2022) found that the foraging and diet of *C. vittatus* differed among size classes and microhabitats. Furthermore, although climbing on vegetation by scorpions constitutes a size-related behavior (Sánchez-Piñero & Urbano-Tenorio 2016 and references therein), no study available has examined whether differences in microhabitat use may also affect predator-prey size relationships in scorpions.

In this paper, we analyze the composition and size-related differences of the diet of *Buthus montanus* Lourenço & Vachon, 2004 in an arid area of SE Spain. *Buthus montanus* is a species included in the *Buthus occitanus* species complex described from the Sierra Nevada mountains (Lourenço & Vachon 2004). The former *B. occitanus* (Amoreux, 1789) currently comprises 78 species distributed throughout southwestern Europe, the Middle East to Iraq, and the northern half of Africa to Cameroon and Kenya (Sousa et al. 2017; Ythier & Lourenço 2022; Rein 2023). Although previous work did not enable accurate identification of the scorpion species inhabiting the Guadix-Baza Basin (see Sousa et al. 2010, 2017), a more recent study has shown that it corresponds to *B. montanus*, the species occurring in arid and mountain habitats of SE Spain (Sousa 2017).

Despite the wide distribution and abundance of the *B. occitanus* species complex in the Mediterranean basin, little information is available on their diet. Le Berre (1979) studied the feeding behavior of *B. occitanus* in captivity. Castilla (1995), Castilla & Pons (2007) and Castilla et al. (2009) provide a qualitative description of *B. occitanus* diet in the Pityusic islands, indicating that it feeds on conspecifics, spiders, tenebrionid beetle larvae as well as other insects, and lizards, without information on the relevance of the different prey in the diet. Skutelsky (1995, 1996) provides information on the hunting of termites, plasticity of foraging, and diet of *Buthus israelis* Shulov & Amitai, 1959 (formerly *B. occitanus* ssp. *israelis)* in the Negev Desert. The work of Sánchez-Piñero & Urbano-Tenorio (2016) offers a description of the diet of *B. montanus* (cited as *B.* cf. *occitanus* due to problems in species identification) in an arid region of SE Spain, in a study analyzing climbing onto vegetation by this scorpion related to prey availability and predation (cannibalism) risk. Therefore, key aspects of the diet of *B. occitanus* species, such as composition, prey selection, size-related variation of the diet, and differences in predator-prey size relationships linked to microhabitat use have not been studied. Within the overall aim of clarifying the diet of *B. montanus*, the specific objectives of this study are: (1) to describe the prey captured by scorpions; (2) to analyze prey selection, considering prey availability at the study site; (3) to examine how sit-and-wait vs. active foraging behavior affects the diet; and (4) to determine variation in diet in relation to scorpion size and analyze the relationship of prey size vs. predator size, taking into account the effect of habitat use (shrub vs. ground).

METHODS

Study area.—The study was conducted at Barranco del Espartal, an ephemeral watercourse (or rambla) located in the arid Guadix-Baza Basin (NE Granada province, Spain; 37.53173°N, 2.69623°W to 37.53603°N, 2.69949°W, 750 m elevation). The climate is Mediterranean continental, with strong temperature fluctuations, both annual (from -14°C in winter to 45°C in summer) and daily (from subzero to 30°C in spring). Rainfall (300 mm mean annual precipitation) occurs mainly in the winter months and is 4.5 times lower than potential evapotranspiration. The soil is composed of silt mixed with gypsum sediment.

The vegetation is an arid open shrub-steppe (58% bare soil, 41% shrub cover) dominated by shrubs (*Artemisia herba-alba* Asso, *A. barrelieri* Bess, *Salsola vermiculata* L., *Retama sphaerocarpa* L., *Gypsophila struthium* Loefl., *Helianthemum squamatum* (L.) Dum. Cours., *H. violaceum* (Cav.) Pers., *Lepidium subulatum* L., *Ononis tridentata* L., *Thymus zygis* L.) and tussock grasses (*Macrochloa tenacissima* (L.) Kunth and *Lygeum spartum* L.). A more detailed description of the study site can be found elsewhere (Doblas-Miranda et al. 2009a).

Diet.—Prey captured by scorpions were recorded during intensive black-light censuses carried out after sunset and up to 3:00 h in six 50 m × 10 m randomly selected plots in September–October 2011 and during the main activity season of the scorpions (June–October) in 2012–2014, 2016 and 2017 (see Sánchez-Piñero & Urbano-Tenorio 2016 for a detailed description of sampling). When a scorpion was detected on the ground or in a shrub, we checked whether it had prey in its pincers or chelicerae. The scorpion was then picked up with forceps and placed in a thick plastic bag. Scorpions seldom dropped their prey when collected, and during the surveys only two scorpions released their prey when enclosed in the bag. We measured the length of each scorpion directly in the field. Scorpions were restrained in a thick, transparent plastic bag and their tails were straightened using forceps. Body length was measured from the chelicerae to the telson, maintaining the telson folded on the metasoma, as most scorpions adopted this position. The total length of each individual was measured to the nearest mm with a small metal ruler. After measurement, each individual was released where it was found.

To detect prey, especially those of small size or substantially digested, we checked the chelicerae of scorpions using an 8X hand magnification lens and sometimes a Canon Eos-550 camera fitted with a 100 mm Canon macro lens. Insects captured by the scorpion due to attraction to black lights were not considered. Prey collected in the field were refrigerated (4°C) for 12–24 h prior to measuring the total body length and fresh weight in the laboratory, and then preserved in 96% ethanol for taxonomic identification. In the case of partially digested prey, total body length was estimated considering the proportions of the remaining body parts with respect to the total body length of live or preserved specimens of the same taxon.

To assess the biomass contribution of different prey and analyze prey-predator size relationships, we determined the fresh weight of both the prey and the scorpions. For this, the prey captured (if still intact) or live individuals of the same taxa (to estimate fresh weight of partially digested prey) were weighed in a precision balance (+/−0.1 mg). The fresh weight of a mantid nymph and a *Scolopendra* were determined by weighing three live individuals of each taxon that were similar in size to the prey. The fresh weight of adult insects (except adult moths and ants) was estimated by weighing 3–10 live individuals of each taxon. To estimate the fresh weight of arachnids, hemimetabolous insects, Lepidoptera (both adults and larvae), and Formicidae (workers and alate adults), 10–26 live specimens of each taxon were collected at the study site. Fresh weight both of the prey and the scorpions was estimated from linear regressions relating $\log_{10}$ body length to $\log_{10}$ fresh weight (see Supplemental Table S1, online at https://doi.org/10.1636/JoA-S-23-008.s1). Because *B. montanus* scorpions could not be accurately weighed in the field (to avoid removing scorpions from the study plots), the fresh weight of the scorpions was estimated by weighing 23 individuals ranging from 14 mm to 65 mm in body length. Live individuals of both the prey and the scorpion were kept refrigerated (4°C) for a maximum of 24 h before being weighed and measured in the laboratory. We considered fresh weight instead of dry weight because we found that the latter usually overestimated sclerotized arthropods but underestimated larvae or arthropods with thin cuticles. In addition, fresh weight accounts also for water provided by the prey, probably a major resource for water-limited desert-dwelling animals such as scorpions.

Prey availability.—Because scorpions captured prey in shrubs, on the ground surface, and below ground (in the litter and a few cm deep in the soil), we used three different methods to assess prey availability: sticky traps in shrubs, sticky traps on the ground, and litter and soil sampling. Prey abundance in shrubs was estimated by means of 10 cm x 10 cm sticky traps covered with tanglefoot adhesive on both sides placed on plants of the 11 shrub species used by

B. montanus (Sánchez-Piñero & Urbano-Tenorio 2016). We placed one trap in five plants of each shrub species once a month from June–July to October in 2012, 2013, 2014 and 2017, but twice a month in August and September 2012. In each sampling, traps were placed in 9–10 arbitrarily assigned plants of randomly assigned shrub species in each plot. Thus, a total of 55 traps were placed in the 11 shrub species per sampling. Sticky traps were placed at sunset and retrieved at dawn in order to collect prey available throughout the period of scorpion activity.

The abundance of epigeal prey was estimated using sticky traps placed on the ground surface. Traps were 5 cm × 20 cm plastic cards covered with tanglefoot adhesive on the upper side. The size of these traps was selected after a preliminary sampling revealed that epigeal arthropods were collected almost exclusively on the periphery of the traps placed on the ground. Sticky traps were placed on the ground once a month from July to October 2014 and June to October 2017. In each sampling, a total of 60 traps (10 traps/plot) were placed under shrubs (30 traps) and on open ground (30 traps) because scorpions forage in both microhabitats. Sticky traps on the ground were placed at sunset and retrieved at dawn in order to collect prey available throughout the period of scorpion activity.

Belowground dwelling arthropods were collected by taking 1000 cm^3 of litter and soil in approximately 20 cm × 10 cm area × 5 cm depth in litter and soft soil sites or 20 cm × 20 cm area × 2.5 cm depth at sites with harder soil. Soil sampling was carried out once per month over the main scorpion activity season from June to October 2014 and 2017. In each sampling, a total of 30 soil samples (5 samples/plot) were collected under the canopy of shrubs (15 samples) and in open areas (15 samples). Sampling was carried out at dusk and during the first two hours of the night. Litter and soil samples were kept in plastic bags and examined in the laboratory, where they were processed using sieves of 1mm mesh size. After sieving, the coarse and fine fractions of litter and soil were placed separately in different 15 × 20 cm white pans and examined to collect the arthropods. This extraction method has been shown to be highly efficient for soil arthropods (Doblas-Miranda et al. 2007, 2009a).

Sampling by the three methods was conducted in the plots where scorpion surveys were already performed on previous nights, or in nearby areas in plots where traps were placed before scorpions were surveyed, in order to avoid disturbing the study plots.

To analyze prey selection by the scorpion, we considered only potential prey measuring ≥ 3 mm body length belonging to the taxa preyed upon by the scorpion at the study site in order to obtain more accurate figures of potential prey availability relative to the scorpion diet. To determine whether prey were captured in shrubs or in the soil (on the ground or below ground) by scorpions, we identified captured prey as either ground or shrub dwellers, since our observations indicated that some scorpions captured prey on the ground but climbed onto shrubs to feed. Prey classification as shrub or ground dwellers was based on information on the arthropod fauna in the study area (see Doblas-Miranda et al. 2007; Sánchez-Piñero et al. 2011; Sánchez-Piñero & Urbano-Tenorio 2016 and references therein), on the information provided by specialists on spiders and hemipterans, and on observations during the present study. For captured prey found both in shrubs and in the soil, we assumed that they were captured in the same place where they were consumed by the scorpions.

Statistical analysis.—Variations in the proportion of scorpions with/without prey (binomial response variable) on shrubs or on the ground (categorical independent variables) were tested using a Chi-square test. The effect of scorpion size (log_{10} fresh weight) on the probability of finding a scorpion with a prey (binomial response variable) was tested by means of a logistic regression using the *glm* function (with a binomial function and logit link) in the *stats* v.4.1.0 R package (R Core Team 2021).

To analyse whether scorpions selected among different potential prey items, we quantified selectivity using the W_i Savage's index. This index is the ratio between the proportion of resources used and the proportion of available resources in the environment, with index values > 1 indicating preference and index values < 1 avoidance (Atienza 1994). Significance of selection was evaluated by the χ^2 test (Krebs 1999), with *a posteriori* correction of significance by the sequential Bonferroni procedure (Holm 1979). Selectivity analyses were conducted separately for prey captured in shrubs, on the ground, and below ground (in the litter and soil), considering potential prey availability in each habitat level. In the case of soil prey, analyses were also carried out separately for sticky traps (epigeal prey) and soil samples (litter and belowground prey). Selectivity analyses were made considering the prey captured by the scorpions only in the surveys conducted when potential prey availability was estimated with a given method (2012–2014 and 2017 for sticky traps on shrubs; June–October 2014 and 2017 for soil sampling and sticky traps on the ground). The proportion of the different types of epigeal and ground-dwelling prey did not differ between the prey included in the selectivity analyses and the remaining prey ($\chi^2 = 4.962$, $P = 0.2913$, d.f. $= 4$, $n = 78$), indicating that the prey included in the analyses are a representative sample of the recorded diet data.

To test whether the proportion of prey in different taxa and trophic guilds (herbivores, detritivores, omnivores, predators) varied with scorpion size, a multinomial logistic regression was performed using the *multinom* function of the *nnet* package in R (Venables & Ripley 2002). The significance of whole models compared with the null models was assessed by means of the Likelihood ratio test. Significance of differences between the proportions of the different prey types and the smallest prey taxon (Hemiptera) captured by different size scorpions was tested by means of Wald Chi-square. Predicted probabilities from the multinomial logistic regression were obtained using the *ggplot2* package in R (Wickham 2016).

Since scorpions captured prey both in the soil and in shrubs, we analyzed the relationship between scorpion size and prey size, and whether this relationship differed between the microhabitats in which the prey were captured (shrub vs. soil). The analysis was conducted by means of a linear regression model considering scorpion size (log_{10} scorpion fresh weight) and microhabitat (ground vs. shrub prey) as explanatory variables, and prey size (log_{10} prey fresh weight) as a response variable. There was no significant effect of the interaction between scorpion size and microhabitat on the explanatory power of the model (comparison between models with and without interaction term: $F = 0.216$, d.f. $= 1, 98$, $P = 0.643$; ANOVA). Size differences (log_{10} fresh weight) between soil- and shrub-dwelling prey were compared by means of an ANOVA. The linear regression analysis and ANOVA test were carried out after testing for normality and homoscedasticity of residuals using the *lm* function in the *stats* v.4.1.0 R package (R Core Team 2021). The comparison between models was performed by means of the *anova* function, also in the *stats* R package.

To test whether larger scorpions used a wider range of prey sizes, we compared the standard deviation of prey sizes (measured as

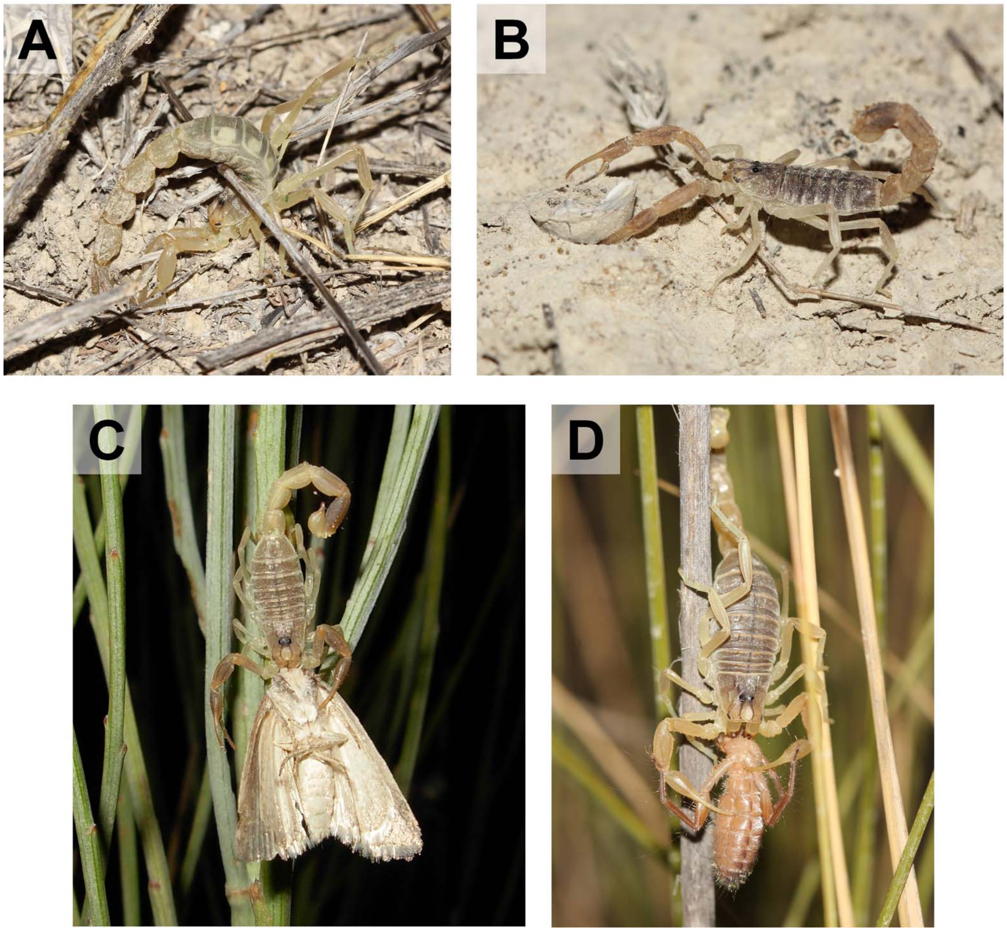

Figure 1.—Prey-capture techniques of *B. montanus*: (A) Capturing a belowground tenebrionid larva by digging into the soil; (B) Opening an *Iberesia* trap door to capture the spider within its burrow; (C) Feeding on a moth captured in a shrub; (D) Feeding on a ground-dwelling *Gluvia dorsalis* solifuge on a shrub.

$\log_{10}$ fresh weight) among scorpion size categories by means of bootstrap. Bootstrapping (100 iterations) of the standard deviations of fresh weights was performed, and the 0.95 confidence intervals for S.D. in each scorpion size category were calculated using the *boot* and *boot.ci* functions of the R package *boot* (Davison & Hinkley 1997; Canty & Ripley 2021).

RESULTS

Overall, we found a total of 131 scorpions with prey, although 18 prey were largely digested by the scorpions and were unidentifiable. Our observations revealed that scorpions captured prey not only on the ground surface, but also below ground and in shrubs. We observed scorpions actively digging into the soil to capture prey, mainly tenebrionid beetle larvae (Fig. 1A), but also to prey on an unidentified hymenopteran inside its burrow. In two cases, scorpions actively searched for prey by digging with their pedipalps in ant-nest mounds, where tenebrionid larvae and embiopterans usually occur. In addition, two scorpions entered the burrows of the nemesiid trap-door spiders *Iberesia* Decae & Cardoso, 2006 and *Nemesia* Audouin, 1846, respectively, lifting the trap doors and capturing the spiders within their burrows (Fig. 1B). Also, we observed scorpions capturing prey in the vegetation, in one case catching a moth in flight that approached the shrub (Fig. 1C), and in other cases a cercopid planthopper jumping inside the shrub canopy and a *Camponotus foreli* ant climbing a shrub. Scorpions also captured moths flying near the ground.

The proportion of scorpions detected capturing or feeding on prey was low. Overall, 6.6% of scorpions were observed with captured prey (131 out of 1984 scorpions), the proportion of scorpions with prey ranging from 4.2% (11 individuals with prey out of 263 scorpions) in 2013 to 8.8% (38 out of 432) in 2017.

The proportion of scorpions with prey in shrubs (13.3%; 74 out of 556 scorpions on shrubs) was higher than the proportion of scorpions with prey on the ground (4.0%; 57 out of 1428 scorpions on the ground) ($\chi^2 = 56.269$, $P < 0.0001$; χ^2 test). However, almost half of the identified prey (34 out of 62 prey, 45%) being eaten by scorpions perched on vegetation were ground-dwelling arthropods, indicating that scorpions usually climbed onto shrubs to feed on ground-captured prey (Fig. 1D).

Diet composition.—The 113 identified prey of *B. montanus* included 55 taxa belonging to 13 orders of Arachnida, Insecta and Chilopoda (see Supplemental Table S2, online at https://doi.org/10.1636/JoA-S-23-008.s1). The main prey in the diet were Araneae, tenebrionid larvae, Formicidae, Embioptera, Hemiptera, and *B. montanus* conspecifics (Table 1), these taxa comprising 77% of the prey. In terms of biomass, the diet was amply dominated by tenebrionid larvae and *B. montanus* conspecifics, these two

Table 1.—Number of prey, percentage of prey, biomass, and percentage of biomass of the main taxa in the diet of *Buthus montanus*.

Taxa	Number of prey	% prey	Biomass (mg)	% Biomass
Araneae	21	18.6	1343	12.19
Buthus montanus	10	8.8	2595	23.55
Coleoptera				
Tenebrionidae larva	20	17.7	3665	33.27
Other Coleoptera	4	3.5	131	1.19
Diptera	1	0.9	—	—
Embioptera	12	10.6	134	1.22
Hemiptera	11	9.7	134	1.22
Hymenoptera				
Formicidae	12	10.6	231	2.10
Other Hymenoptera	2	1.8	21	0.19
Lepidoptera				—
Adult	9	8.0	458	4.16
Larva	4	3.5	1544	14.01
Mantodea	1	0.9	3	0.03
Raphidioptera larva	1	0.9	—	—
Scolopendromorpha	1	0.9	244	2.21
Solifugae	2	1.8	502	4.56
Zygentoma	2	1.8	12	0.11
Total	113		11017	

prey items comprising more than 55% of the biomass. Araneae and Lepidoptera larvae constituted also important groups in terms of biomass.

From a trophic perspective, predators and detritivores comprised the highest proportions of prey (34.5% and 31% of the total number of prey, respectively) and biomass (43.9% and 36.8% %, respectively) in the diet (Table 1; Supplemental Table S2).

The selectivity analysis showed that tenebrionid larvae and *B. montanus* conspecifics were very positively selected epigeal and ground prey, when potential prey availability determined from ground sticky traps and soil sampling were considered, respectively (Table 2). Prey selectivity in shrubs indicated a significant positive selection for *B. montanus* conspecifics and Formicidae.

Diet variations with scorpion size.—The probability of finding a scorpion with a prey did not vary with scorpion size ($z = -0.159$, $P = 0.874$; logistic regression). By contrast, the composition of the diet of *B. montanus* changed in relation to scorpion size. The frequency of Hemiptera prey decreased with increasing scorpion size, while the opposite was found for the *B. montanus* conspecifics and tenebrionid larvae (Likelihood ratio test = 19.293, d.f. = 6, $P = 0.0037$; multinomial logistic regression; Fig. 2; Supplemental Table S3, online at https://doi.org/10.1636/JoA-S-23-008.s1). However, the proportion of prey of different trophic guilds (predators, omnivores, herbivores, detritivores) did not change with scorpion size (Likelihood ratio test = 1.048, d.f. = 3, $P = 0.790$; multinomial logistic regression). Within predatory prey, a significant increase was found in the proportion of conspecifics with increasing scorpion size ($z = 2.283$, $P = 0.0224$; logistic regression).

Prey size vs. predator size.—A large overlap in prey size was found across scorpion size categories, since small 14–20 mm scorpions were able to capture prey 3–25 mm (1.5–263 mg), while medium 31–40 mm scorpions captured prey 3–40 mm (3–368 mg), and large 51–70 mm scorpions captured prey 6–44 mm length (14–779 mg). However, prey size variability differed significantly among scorpion size categories, the larger 41–50 and 51–70 mm scorpions showing a significantly larger standard deviation of prey fresh weight than 14–20, 21–30 and 31–40 mm scorpion size categories (Fig. 3). We found a pattern of increasing prey size ($\log_{10}$ fresh weight of prey) with increasing scorpion size ($\log_{10}$ fresh weight of scorpions) (Fig. 4; Supplemental Table S4, online at https://doi.org/10.1636/JoA-S-23-008.s1). This relationship was also significantly affected by the microhabitat where the prey were captured, prey size being significantly smaller in shrubs than on the ground for scorpions of a given size. In fact, captured shrub-dwelling prey were significantly smaller (18.3 ± 6.5 mg) than captured soil-dwelling prey (136.8 ± 23.4 mg; F = 31.292, d.f. = 1, 103, $P < 0.0001$; ANOVA).

Table 2.—Selectivity of prey captured by *B. montanus* on the ground and in shrubs considering the different sampling methods. Asterisks indicate significant *P* values after sequential Bonferroni correction.

Prey	% use	% avail.	w_i	se (w_i)	Chi^2	*P*
Ground prey (n = 40) vs. soil sampling						
Araneae	20.00	13.57	1.47	0.36	1.743	0.1868
B. montanus	12.50	0.45	27.78	1.08	609.733	<0.0001*
Embioptera	17.50	22.17	0.79	0.37	0.332	0.5646
Tenebrionidae larva	30.00	3.17	9.46	0.44	364.461	<0.0001*
Other Arthropoda	20.00	60.63	0.33	0.32	4.363	0.0367
Ground prey (n = 40) vs. ground sticky traps						
Araneae	20.00	37.08	0.54	0.33	1.995	0.1578
B. montanus	12.50	3.00	4.17	0.54	33.866	<0.0001*
Embioptera	17.50	11.24	1.56	0.38	2.104	0.1469
Tenebrionidae larva	30.00	0.37	81.08	1.03	6011.213	<0.0001*
Other Arthropoda	20.00	48.31	0.41	0.32	3.302	0.0692
Shrub prey (n = 24) vs. shrub sticky traps						
Araneae	20.83	12.39	1.68	0.30	5.074	0.0243
B. montanus	8.33	0.15	55.53	1.11	2416.512	<0.0001*
Formicidae	29.17	10.91	2.67	0.25	43.846	<0.0001*
Hemiptera	25.00	53.54	0.47	0.26	4.363	0.0367
Other Arthropoda	16.70	23.00	0.73	0.27	1.011	0.3147

DISCUSSION

The diet composition of *B. montanus* characterizes it as a generalist predator that feeds on a diverse array of prey, as reported in previous studies of different scorpion species (Polis 1979; Polis & McCormick 1986b; Yamashita 2004; Novruzov 2017a, b). In fact, the proportion of taxa represented by unique captures in the diet of *B. montanus* (65%) was similar to the proportion of unique taxa found in the more extensive prey record of *S. mesaensis* (58%; Polis 1979), indicating a highly opportunistic feeding in both scorpion species. Our data also show that spiders, other arachnids, tenebrionid larvae, and both adult and larval Lepidoptera, as well as cannibalized conspecifics, appear in the diet of *B. montanus*, as indicated for *B. occitanus* from the Columbretes islands (Castilla & Pons 2007). The lack of adult tenebrionid beetles in the diet of *B. montanus* contrasts with the prevalence of these beetles in the diet of *S. mesaensis* (comprising 41.5% of the number of prey and > 17% of the biomass; Polis 1979). Although tenebrionids are a dominant group with crepuscular or strictly nocturnal activity during the summer months in the study area (Sánchez-Piñero 1994; Hódar & Sánchez-Piñero 2002; Sánchez-Piñero et al. 2011; González-Megías et al. 2011) and were commonly observed in the study plots during our night censuses, adults of most species are probably too

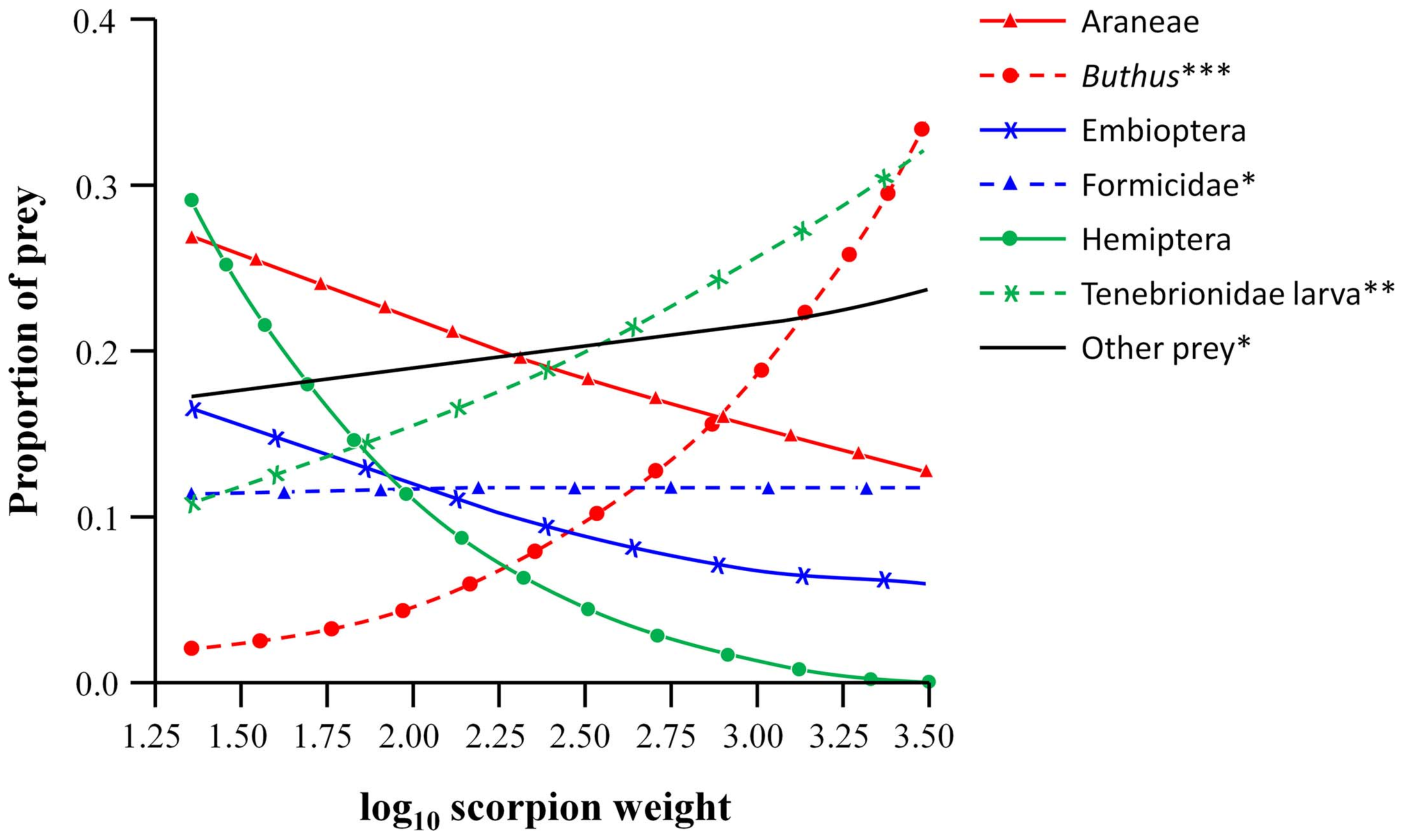

Figure 2.—Logistic multinomial regression of the proportion of prey captured by *B. montanus* scorpions in relation to scorpion size ($\log_{10}$ scorpion weight). Comparisons between prey taxa with respect to Hemiptera as baseline group: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

large and sclerotized to be preyed upon by *B. montanus*. The lack of termites in the diet of *B. montanus* in our study, in contrast to the findings of Skutelsky (1995), is due to the scarcity of termites in the study area (Doblas-Miranda et al. 2007; Sánchez-Piñero et al. 2011). However, in agreement with Skutelsky (1995), our results highlight the flexibility of foraging in *Buthus* scorpions.

Hunting strategies of *B. montanus* are diverse due to their ability to capture prey on the ground surface, below ground and in vegetation. Although most *B. montanus* scorpions were sit-and-wait foragers on the ground, about 25% of the individuals, mostly smaller scorpions, climbed shrubs (Sánchez-Piñero et al. 2013; Sánchez-Piñero & Urbano-Tenorio 2016), a behavior also reported in other scorpion species (see Sánchez-Piñero & Urbano-Tenorio 2016 and references therein). Although shrub climbing appears to be related to cannibalism avoidance in *B. montanus* (Sánchez-Piñero & Urbano-Tenorio 2016), scorpions capture prey in shrubs, as revealed by direct observations in the present study (e.g., capture of a flying adult moth and a jumping Cercopidae in shrub canopies, as well as foraging *Camponotus foreli* ants in shrubs), and, indirectly, by the occurrence of shrub-dwelling arthropods such as epiphytic spiders and hemipterans in the diet of the scorpion. In addition, active foraging was observed during our study. As reported in other scorpion species (Polis 1979; Ojanguren-Affilastro et al. 2016), *B. montanus* was seen entering trap-door spider burrows to capture Nemesiidae, in addition to preying on tenebrionid beetle larvae and a solitary bee from inside their burrows in the soil, and actively searching for tenebrionid larvae by digging into litter accumulations of ant-nest mounds.

Despite its generalist diet, *B. montanus* shows a strong selection for some prey, especially tenebrionid larvae and other scorpions. This result contrasts with the weak selectivity values found for most prey in *M. eupeus* (Novruzov 2017a). Although tenebrionid larvae and *B. montanus* conspecifics appeared significantly and positively selected in the analysis using different methods to estimate prey availability, biases associated with those methods should be considered in interpreting these results. The percentage of tenebrionid larvae was almost ten-fold higher in litter/soil samples than in sticky traps, a result that was expected due to their mainly belowground activity (Matthews et al. 2010). These results coincide with those obtained in extensive litter and belowground sampling conducted in the study area (Doblas-Miranda et al. 2007, 2009b), indicating that scorpions actively captured most tenebrionid larvae by digging in the litter and soil. Our observations of active foraging for tenebrionid larvae in ant-nest mounds strongly support the above results. In the case of *B. montanus*, sticky traps as well as litter/soil sampling may underestimate scorpion abundance. Scorpions active on the soil surface are probably able to escape when litter/soil samples are collected, but the method was intended to measure abundance of prey occurring inside the litter and soil, where we actually expected to find a very low abundance of scorpions (as they usually shelter in deeper burrows). Regarding sticky traps, this interception method depends on species vagility, likely underestimating the abundance of predominantly sit-and-wait foraging scorpions moving within a limited territory (e.g., the majority of individuals occur within 1 m from their burrows in *S. mesaensis*; Polis et al. 1985). However, these results also indicate that the availability of wandering scorpions

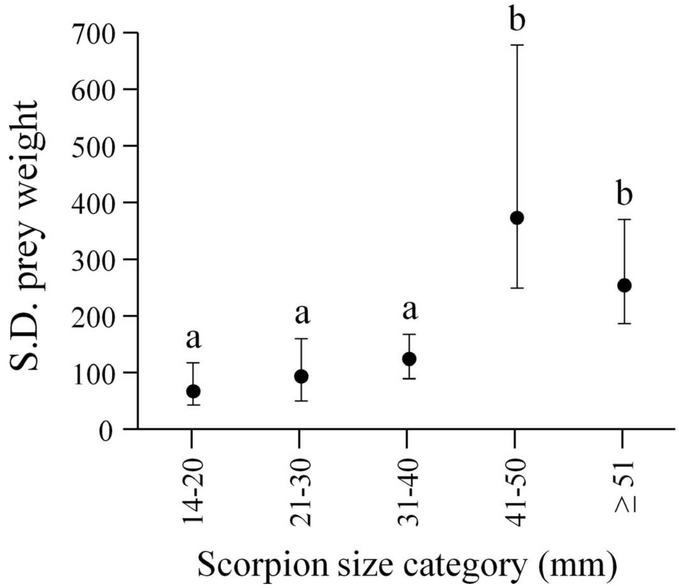

Figure 3.—Standard deviation and 95% confidence interval of prey weight for the different size categories of *B. montanus* scorpions from bootstrapping (100 iterations). Different letters on top of each bar indicate significant differences in standard deviation values.

is low, suggesting that the 4-fold higher proportion of conspecifics in the diet of *B. montanus* is due to active search of larger individuals for juveniles. Climbing into shrubs related to a predator (cannibal)-avoidance mechanism in *B. montanus* (Sánchez-Piñero & Urbano-Tenorio 2016) supports this argument. Strikingly, *B. montanus* conspecifics and tenebrionid larvae comprise more than half of the biomass consumed by the scorpions. Our results reveal the importance of knowing the foraging behavior of the predator as well as using complementary sampling methods to assess the availability and habits of the prey (Polis 1979; Brown & O'Connell 2000; Harwood et al. 2001).

Notably, predatory arthropods (including both intraguild prey and conspecifics) constituted the dominant component of the diet of *B. montanus* in our study area. Intraguild predation and cannibalism are important trophic interactions, especially in scorpions and spiders (Polis 1981; Polis & McCormick 1986a; Polis et al. 1989; Wise 1993; Arim & Marquet 2004). Intraguild predation (excluding cannibalism) represented 25% of prey and 20.5% of the biomass consumed by *B. montanus*, a proportion within the reported range in the diet of other scorpion species (Polis 1979; Polis & McCormick 1986a, 1987; Yamashita 2004; McReynolds 2008, 2020; Novruzov 2017a, b) and spiders (Hodge 1999). A comparison with two large spiders in the study area indicates that intraguild predation (excluding cannibalism) is much higher in *B. montanus* than in *Eresus kollari* Rossi, 1846 (Eresidae) (0.6% of the prey) and *Latrodectus lilianae* Melic, 2000 (Theridiidae) (3.8–14.2% of the prey, and 2.4–16.2% of biomass) (Hódar & Sánchez-Piñero 2002; Pérez-Zarcos & Sánchez-Piñero 2016). Field experiments have also shown that intraguild predation by scorpions is a major factor determining the distribution and abundance of other predatory arthropods, such as spiders and other scorpion species (Polis & McCormick 1986a, 1987).

Cannibalism also constituted a major part of the diet of *B. montanus* at our study site. Our results are similar to those reported for *S. mesaensis*, in which cannibalism constituted 9% of the prey

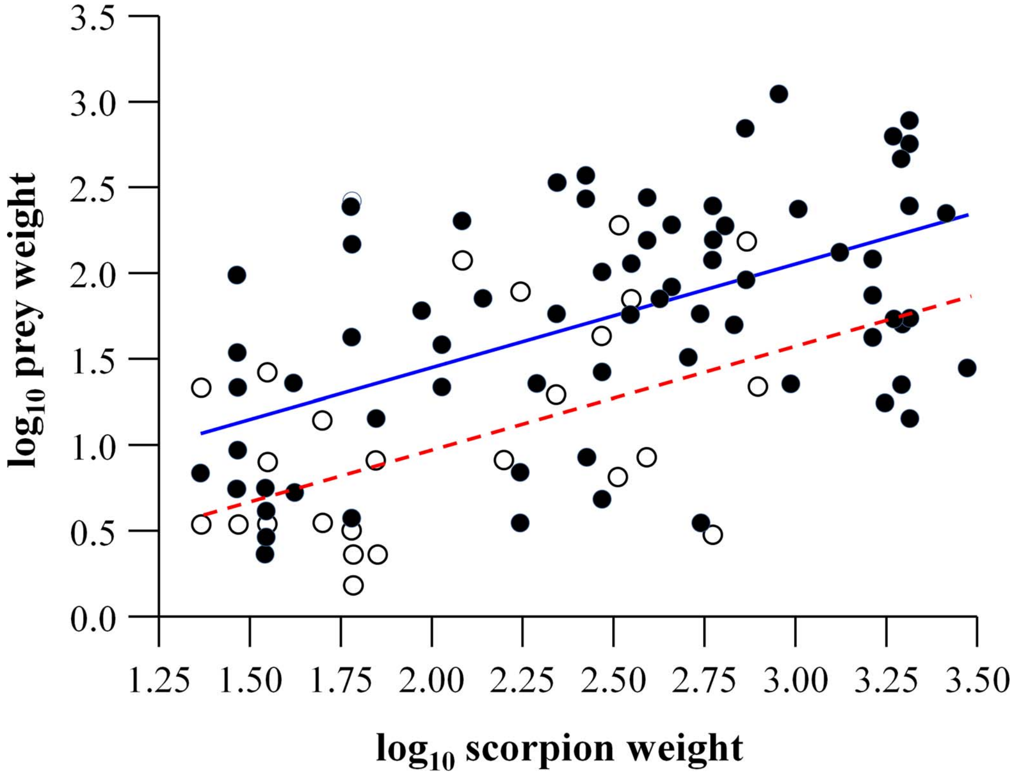

Figure 4.—Prey size ($\log_{10}$ prey weight) relationship with scorpion size ($\log_{10}$ scorpion weight) in soil (solid circles, solid blue line) and shrub microhabitats (white circles, broken red line).

and 28.4% of the ingested biomass (Polis 1979). Our results support the contention that cannibalism is a key interaction that shapes scorpion ecology and behavior (Polis 1990; Sánchez-Piñero & Urbano-Tenorio 2016). Scorpions may perform a crucial role as key predators, especially in desert ecosystems (Polis 1991).

Prey size appears also as an important factor determining the diet of *B. montanus*, as previously indicated in *S. mesaensis* and *M. gibbosus* (Polis 1984; Kaltsas et al. 2008). In this sense, our data indicate that the minimum prey size is 3 mm; Smaller prey were not recorded in our surveys. Although this result could be due to a bias in our ability to detect prey smaller than 3 mm, evidence supports the idea that arthropods < 3 mm are rarely or never captured by *B. montanus*. In addition, over the entire study, we actually detected a number of scorpions with partially digested prey whose remains measured 1–2 mm in length (some of the unidentified prey plus a few prey whose remains could still be identified).

As in most predators, *B. montanus* showed ontogenetic diet variation related to differences in prey size and composition. Firstly, larger individuals not only feed on larger prey in average, but also show a larger range of prey sizes, a pattern previously indicated in the sand dune scorpion *S. mesaensis* (Polis 1984), and generally found in predators (Cohen et al. 1993; Nakazawa et al. 2011, 2013). Secondly, scorpions in vegetation, being mostly small, young individuals, captured smaller prey than did small scorpions on the ground (see also Sánchez-Piñero & Urbano-Tenorio 2016 and references therein). Ontogenetic changes in habitat use are often related with shifts in predator-prey size relationships (Werner & Gilliam 1984; Dahlgren & Eggleston 2000; Griffiths 2020).

The frequency of different prey items varied with scorpion size, as found in other scorpion species (Polis 1979, 1984; Polis & McCormick 1986a; McReynolds 2020). Thus, Hemiptera appeared with a higher proportion in the diets of smaller scorpions, while cannibalism occurred mainly in large scorpions. These results are linked with two size-related aspects of *B. montanus*. First, our data revealed a positive relationship between scorpion size and prey size. Thus, smaller scorpions tend to feed on smaller prey such as Hemiptera, which included the smallest recorded prey items. Second, previous works in the study area have shown that shrub climbing is also size-related, the probability to find a scorpion on a shrub being inversely related to its size (Sánchez-Piñero et al. 2013; Sánchez-Piñero & Urbano-Tenorio 2016). It bears mentioning that hemipterans and smaller spiders are dominant arthropods in shrub canopies in the study area (Sánchez-Piñero 1994; this study), increasing the probability that small scorpions prey on these taxa (e.g., hemipterans constitute 25% of shrub dwelling prey but only 4% of soil prey). Thus, the risk of cannibalism by larger scorpions becomes an important factor determining where younger scorpions can feed safely, affecting trophic interactions.

In turn, climbing vegetation by smaller scorpions likely enhances the connection between the soil and plant-canopy food-web compartments (i.e., belowground-aboveground interactions; e.g., Wardle et al. 2004). Some studies have stressed how aboveground food webs are subsidized by belowground prey (Polis 1991; Miyashita et al. 2003; Haraguchi et al. 2013). However, our results indicate that climbing vegetation by smaller *B. montanus* scorpions, a behavior related to cannibalism avoidance in this species, can also increase predation (and predation risk) of shrub-dwelling arthropods, such as epiphytic spiders and hemipterans, due to scorpion foraging at the aboveground (plant canopy) level (see Schmidt-Entling & Siegenthaler 2009 for both direct and indirect effects of predator occurrence on prey densities). Climbing vegetation by other scorpion species such as *B. israelis*, *S. mesaensis*, *C. vittatus*, and the bothriurid *Brachistosternus ferrugineus* (Thorell, 1876) (Polis 1979; Skutelsky 1996; Brown & O'Connell 2000; McReynolds 2008, 2022; Nime et al. 2016) for different reasons (predation and/or competition avoidance, foraging optimization; McReynolds 2022) suggest that this role connecting the soil and aboveground food-web compartments may occur widely in scorpions. These findings show that interactions between soil and aboveground food-web compartments may be more diverse and complex than currently reported, regarding not only belowground prey subsidies to aboveground predators but also an increase in predation pressure at the plant-canopy level from the soil food chain.

In conclusion, our data show that *B. montanus* is a generalist predator able to capture prey on the ground surface, below ground and in shrub canopies. Although the diet includes a diverse array of prey, the scorpion feeds mainly on predatory arthropods and tenebrionid beetle larvae. Cannibalism is a major component in the diet of this scorpion species, accounting for almost one fourth of the biomass ingested, especially in large scorpions. The risk of cannibalism is related partially to ontogenetic diet variation, as climbing vegetation to reduce the risk of cannibalism appears to be related to changes in diet composition, prey size, and predator-prey size relationships in smaller scorpions. Further field and experimental work will be necessary to uncover the role of cannibalism in the behavior and trophic ecology of scorpions and their consequences on food-web structure and dynamics.

ACKNOWLEDGMENTS

We thank Guillermo García Franco and Francisco Jesús Martín García for their help in the field work. Manuel Baena, Francisco Javier Pérez López, Laura Pérez Zarcos and Alberto Tinaut kindly identified Hemiptera, Lepidoptera, Araneae and Formicidae. Comments by Yael Lubin and two anonymous reviewers enhanced the manuscript. We thank David Nesbitt for linguistic advice. Permission from the owners of Barranco del Espartal and research permits from the Consejería de Agricultura, Pesca y Medio Ambiente, Junta de Andalucía, allowed us to conduct this research.

SUPPLEMENTAL MATERIALS

Supplemental Tables S1-S4, available online at https://doi.org/10.1636/JoA-S-23-008.s1

Table S1.—Regression parameters to estimate fresh weight from body length.

Table S2.—Taxa, trophic group, microhabitat, and number of prey captured by *B. montanus* during its main activity season.

Table S3.—Results of a logistic multinomial regression for the proportion of prey captured by *B. montanus* in relation to scorpion size.

Table S4.—Results of the linear model for the effects of scorpion size scorpion and microhabitat on prey size.

LITERATURE CITED

Arim M, Marquet PA. 2004. Intraguild predation: a widespread interaction related to species biology. *Ecology Letters* 7:557–564.

Atienza JC. 1994. La utilización de índices en el estudio de la selección de recursos. *Ardeola* 41:173–175.

Brown CA, O'Connell DJ. 2000. Plant climbing behavior in the scorpion *Centruroides vittatus*. *American Midland Naturalist* 144:406–418.

Canty A, Ripley BD. 2021. boot: Bootstrap R (S-Plus) Functions. R package version 1.3–28.

Casper CS. 1985. Prey capture and stinging behavior in the emperor scorpion, *Pandinus imperator* (Koch) (Scorpiones, Scorpionidae). *Journal of Arachnology* 13:277–283.

Castilla AM. 1995. Interactions between lizards *(Podarcis hispanica atrata)* and scorpions *(Buthus occitanus)* in the Columbretes Islands. *Bolletí de la Societat d'Història Natural de les* Balears 38:47–50.

Castilla AM, Pons GX. 2007. Primeros datos sobre la población de escorpiones *(Buthus occitanus)* en las islas Columbretes (Mediterráneo, España). *Bolletí de la Societat d'Història Natural de les Balears* 50:257–268.

Castilla AM, Herrel A, Gosá A. 2009. Predation by scorpions (*Buthus occitanus*) on *Podarcis atrata* from the Columbretes islands. *Munibe* 57:299–302.

Chippaux JP, Goyffon M. 2008. Epidemiology of scorpionism: A global appraisal. *Acta Tropica* 107:71–79.

Cloudsley-Thompson JL. 1990. Scorpions in mythology, folklore, and history. Pp. 462–485. *In* The Biology of Scorpions. (G.A. Polis, ed.). Stanford University Press, Stanford, California.

Cohen JE, Pimm SL, Yodzis P, Saldaña J. 1993. Body sizes of animal predators and animal prey in food webs. *Ecology* 62:67–78.

Dahlgren CP, Eggleston DB. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81:2227–2240.

Davison AC, Hinkley DV. 1997. Bootstrap Methods and their Applications. Cambridge University Press, Cambridge. https://statwww.epfl.ch/davison/BMA/

Doblas-Miranda E, Sánchez-Piñero F, González-Megías A. 2007. Soil macroinvertebrate fauna of a Mediterranean arid system: Composition and temporal changes in the assemblage. *Soil Biology & Biochemistry* 39:1916–1925.

Doblas-Miranda E, Sánchez-Piñero F, González-Megías A. 2009a. Different microhabitats affect soil macroinvertebrate assemblages in a Mediterranean arid ecosystem. *Applied Soil Ecology* 41:329–335.

Doblas-Miranda E, Sánchez-Piñero F, González-Megías A. 2009b. Vertical distribution of soil macrofauna in an arid ecosystem: Are litter and belowground compartmentalized habitats? *Pedobiologia* 52:361–373.

Eubanks MD, Denno RF. 2000. Health food versus fast food: The effects of prey quality and mobility on prey selection by a generalist predator and indirect interactions among prey species. *Ecological Entomology* 25: 140–146.

González-Megías A, Sánchez-Piñero F, Hódar JA. 2011. Trophic interactions in an arid ecosystem: From decomposers to top predators. *Journal of Arid Environments* 75:1333–1341.

Griffiths D. 2020. Foraging habitat determines predator-prey size relationships in marine fishes. *Journal of Fish Biology* 97:964–973.

Haraguchi TF, Uchida M, Shibata Y, Tayasu I. 2013. Contributions of detrital subsidies to aboveground spiders during secondary succession, revealed by radiocarbon and stable isotope signatures. *Oecologia* 171: 935–944.

Harwood JD, Sunderland KD, Sydmondson WOC. 2001. Living where the food is: web location by linyphiid spiders in relation to prey availability in winter wheat. *Journal of Applied Ecology* 38:88–99.

Hódar JA, Sánchez-Piñero F. 2002. Feeding habits of the black widow spider *Latrodectus lilianae* (Araneae: Theridiidae) in an arid zone of SE Spain. *Journal of Zoology* 257:101–109.

Hodge MA. 1999. The implications of intraguild predation for the role of spiders in biological control. *Journal of Arachnology* 27:351–362.

Holm S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6:65–70.

Kaltsas D, Stathi I, Mylonas M. 2008. The foraging activity of *Mesobuthus gibbosus* (Scorpiones: Buthidae) in central and south Aegean archipelago. *Journal of Natural History* 42:513–527.

Krebs CJ. 1999. Ecological Methodology. 2nd ed. Benjamin/Cummings-Addison Wesley Longman, Menlo Park, California.

Le Berre M. 1979. Analyse séquentielle du comportement alimentaire du scorpion *Buthus occitanus* (Amor.) (Arach. Scorp. Buth.). *Biology of Behaviour* 4:97–122.

Lourenço WR, Vachon M. 2004. Considérations sur le genre *Buthus* Leach, 1815 en Espagne, et description de deux nouvelles espèces (Scorpiones, Buthidae). *Revista Ibérica de Aracnología* 9:81–94.

Matthews EG, Lawrence JF, Bouchard P, Steiner WE, Ślipiński A. 2010. 11.14. Tenebrionidae Latreille, 1802. Pp. 574–659. *In* Coleoptera, Beetles. Volume 2. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). (W Kükenthal, RAB Leschen, RG Beutel, JF Lawrence, eds.). De Gruyter, Berlin.

McCormick SJ, Polis GA. 1991. Prey, predators, and parasites. Pp 294–320. *In* The Biology of Scorpions. (G.A. Polis, ed.). Stanford University Press, Stanford, California.

McReynolds CN. 2008. Microhabitat preferences for the errant scorpion, *Centruroides vittatus* (Scorpiones, Buthidae). *Journal of Arachnology* 36:557–564.

McReynolds CN. 2020. Effect of season and scorpion size on the foraging and diet of the striped bark scorpion, *Centruroides vittatus* (Buthidae: Scorpiones) in blackbrush habitat of south Texas. *Euscorpius* 323:1–16.

McReynolds CN. 2022. The effect of microhabitat use on the foraging and diet of the striped bark scorpion, *Centruroides vittatus* (Buthidae: Scorpiones) in blackbrush habitat of south Texas. *Journal of Arachnology* 50:90–100.

Miranda RJ, Bermúdez S, Cleghorn J, Cambra RA. 2015. Presas de escorpiones (Arachnida: Scorpiones) de Panamá, con observaciones sobre el comportamiento de depredación. *Revista Ibérica de Aracnología* 27:115–123.

Miyashita T, Takada M, Shimazaki A. 2003. Experimental evidence that aboveground predators are sustained by underground detritivores. *Oikos* 103:31–36.

Mukherjee S, Heithaus M. 2013. Dangerous prey and daring predators: a review. *Biological Reviews* 88:550–563.

Nakazawa T, Ohba S, Ushio M. 2013. Predator-prey body size relationships when predators can consume prey larger than themselves. *Biological Letters* 9: 20121193. doi:10.1098/rsbl.2012.1193

Nakazawa T, Ushio M, Kondoh M. 2011. Scale dependence of predator-prey mass ratio: Determinants and applications. *Advances in Ecological Research* 45:269–302.

Nime MF, Casanoves F, Mattoni CI. 2016. Microhabitat use and behavior differ across sex-age classes in the scorpion *Brachistosternus ferrugineus* (Scorpiones: Bothriuridae). *Journal of Arachnology* 44:235–244.

Novruzov NE. 2017a. Notes on night activity and trophic behaviour of *Mesobuthus eupeus* (S.L. Koch, 1839) (Arachnida, Scorpiones, Buthidae) in the Eastern Azerbaijan. *Euroasian Entomological Journal* 16:67–72.

Novruzov NE. 2017b. Comparison of trophic spectra and hunting strategies of some large arachnids (Arachnida: Scorpiones, Solifugae, Aranei) in semi-desert biocenoses of Gobustan (Eastern Azerbaijan). *Caucasian Entomological Bulletin* 13:135–144.

Ojanguren-Affilastro AA, Botero-Trujillo R, Castex A, Pizarro-Araya J. 2016. Biological aspects of the genus *Brachistosternus* (Bothriuridae) in the Atacama Desert (Chile), with the description of a new type of pedipalp macroseta. *Gayana* 80:169–174.

Pérez-Zarcos L, Sánchez-Piñero F. 2016. Diet of the ladybird spider *Eresus kollari* (Araneae: Eresidae) in an arid system of southeastern Spain. *Journal of Arachnology* 44:359–366.

Polis GA. 1979. Prey and feeding phenology of the desert sand scorpion *Paruroctonus mesaensis* (Scorpionidae: Vaejovidae). *Journal of Zoology* 188:333–346.

Polis GA. 1981. The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics* 12:225–251.

Polis GA. 1984. Age structure component of niche width and intra-specific resource partitioning: Can age groups function as ecological species? *American Naturalist* 123:541–564.

Polis GA. 1990. Ecology. Pp. 247–293. *In* The Biology of Scorpions. (GA Polis, ed.). Stanford University Press, Stanford, California.

Polis GA. 1991. Complex interactions in deserts: an empirical critique of food web theory. *American Naturalist* 138:123–155.

Polis GA, McCormick SJ. 1986a. Scorpions, spiders and solpugids: predation and competition among distantly related taxa. *Oecologia* 71:111–116.

Polis GA, McCormick SJ. 1986b. Patterns of resource use and age structure among species of desert scorpion. *Journal of Animal Ecology* 55:59–73.

Polis GA, McCormick SJ. 1987. Intraguild predation and competition among desert scorpions. *Ecology* 68:332–343.

Polis GA, McReynolds CN, Ford RG. 1985. Home range geometry of the desert scorpion *Paruroctonus mesaensis. Oecologia* 67:273–277.

Polis GA, Yamashita T. 1991. The ecology and importance of predaceous arthropods in desert communities. Pp. 180–222. *In* The Ecology of Desert Communities. (GA Polis, ed.). University of Arizona Press, Tucson, Arizona.

Polis GA, Myers CA, Holt RD. 1989. The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20:297–330.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Rein JO. 2023. The Scorpion Files. Trondheim: Norwegian University of Science and Technology. Online at https://www.ntnu.no/ub/scorpion-files/, accessed on 2023.01.11.

Rodríguez-Cabrera TM, Morell Savall E, Teruel R. 2021. Amphibians and reptiles as prey of *Heteroctenus junceus* (Scorpiones: Buthidae), with a summary of vertebrate predation by scorpions in the West Indies. *Euscorpius* 342:1–6.

Sánchez-Hernández J, Nunn AD, Adams C E, Amundsen PA. 2019. Causes and consequences of ontogenetic dietary shifts: A global synthesis using fish models. *Biological Reviews* 94:539–554.

Sánchez-Piñero F. 1994. Ecología de las comunidades de coleópteros en zonas áridas de la Depresión de Guadix-Baza (Sureste de la Península Ibérica). PhD Thesis, Universidad de Granada.

Sánchez-Piñero F, Urbano-Tenorio F. 2016. Watch out for your neighbor: Climbing onto shrubs is related to risk of cannibalism in the scorpion *Buthus* cf. *occitanus*. *PLoS ONE* 11(9): e0161747. doi:10.1371/journal.pone.0161747

Sánchez-Piñero F, Tinaut A, Aguirre-Segura A, Miñano J, Lencina JL, Ortiz-Sánchez FJ. et al. 2011. Terrestrial arthropod fauna of arid areas of SE Spain: Diversity, biogeography, and conservation. *Journal of Arid Environments* 75:1321–1332.

Sánchez-Piñero F, Urbano-Tenorio F, Martín-García FJ 2013. Foraging of *Buthus occitanus* (Scorpiones: Buthidae) on shrub branches in an arid area of southeastern Spain. *Journal of Arachnology* 41:88–90.

Santos MSV, Silva CGL, Silva-Neto B, Grangeiro CRP, Lopes VHG, Teixeira AG. et al. 2016. Clinical and epidemiological aspects of scorpionism in the World: A systematic review. *Wilderness & Environmental Medicine* 27:504–518.

Schmidt-Entling MH, Siegenthaler E. 2009. Herbivore release through cascading risk effects. *Biology Letters* 5:773–776.

Shachak M, Brandt S. 1983. The relationship between sit and wait foraging strategy and dispersal in the desert scorpion, *Scorpio maurus. Oecologia* 60:371–377.

Skutelsky O. 1995. Flexibility in foraging tactics of *Buthus occitanus* scorpions, as a response to aboveground activity of termites. *Journal of Arachnology* 23:46–48.

Skutelsky O. 1996. Predation risk and state-dependent foraging in scorpions: effects of moonlight on foraging in the scorpion *Buthus occitanus*. *Animal Behavior* 52:49–57.

Sousa P. 2017. Resilient arthropods: *Buthus* scorpions as a model to understand the role of past and future climatic changes on Iberian Biodiversity. PhD Thesis, University of Porto.

Sousa P, Arnedo MA, Harris DJ. 2017. Updated catalogue and taxonomic notes on the Old-World scorpion genus *Buthus* Leach, 1815 (Scorpiones, Buthidae). *ZooKeys* 686:15–84.

Sousa P, Froufe E, Alves PC, Harris DJ. 2010. Genetic diversity within scorpions of the genus *Buthus* from the Iberian Peninsula: mitochondrial DNA sequence data indicate additional distinct cryptic lineages. *Journal of Arachnology* 38:206–211.

Suzuki Y, Ikemoto M, Yokoi T. 2022. The ontogenetic dietary shift from non-dangerous to dangerous prey in predator-eating predators under capture risk. *Ecology and Evolution* 12: e9609. https://doi.org/10.1002/ece3.9609

Symondson WOC, Sunderland KD, Greenstone MH. 2002. Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* 47:561–594.

Toscano-Gadea CA, Costa FG. 2006. Is *Tityus uruguayensis* (Buthidae) an araneophagic scorpion? An experimental analysis of its predatory behaviour on spiders and insects. *Bulletin of the British arachnological Society* 13:256–264.

Venables WN, Ripley BD. 2002. Modern Applied Statistics with S, Fourth edition. Springer, New York. https://www.stats.ox.ac.uk/pub/MASS4/

Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH, Wall DH. 2004. Ecological linkages between aboveground and belowground biota. *Science* 304:1629–1633.

Werner EE, Gilliam JF. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425.

Wickham H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. https://ggplot2.tidyverse.org

Wise DH. 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge.

Yamashita T. 2004. Surface activity, biomass, and phenology of the striped scorpion, *Centruroides vittatus* (Buthidae) in Arkansas, USA. *Euscorpius* 17:25–33.

Ythier E, Lourenço WR. 2022. First record of the genus *Buthus* Leach, 1815 from Kenya (Scorpiones: Buthidae) and description of a new species. *Serket* 19:1–6.

Manuscript received 24 February 2023, revised 4 July 2023, accepted 18 July 2023.