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Microhabitat selection in the sand recluse spider (*Sicarius thomisoides*): the effect of rock size and temperature

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ABSTRACT

In spiders, temperature is considered an important environmental variable for microhabitat selection. In this study, we evaluated the effect of temperature and rock size on the presence of the sand recluse spider *Sicarius thomisoides* and the degree of selectivity in different locations. This species is a large spider that lives under rocks in desert and semi-desert climates and is particularly active during the summer. In Chile, these spiders can be found at both coastal and inland locations under different thermal conditions, where usually the temperatures are lower near the coast. If large-scale climatic conditions are important for this species, they may be expected to select lower rock temperatures on the coast than at inland locations. In addition, we would expect that the spiders would choose larger rocks in inland compared to coast locations, which reduce the effect of high temperatures. We found that the probability of finding individuals of this species increased according to rock temperature and rock size in the field. Our results suggest that *S. thomisoides* prefers larger and warmer rocks to shelter under during the day, this selectivity being similar at both coastal and inland locations. Thus, this species tends to select rocks with the same thermal and structural conditions, independent of the climatic conditions.

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Spider; habitat selection; selectivity; temperature; rock size

Introduction

Habitat includes the resources and conditions necessary for the survival and reproduction of individuals present in an area (Hall et al. 1997; Krausman 1999). Habitat selection can be defined as a 'hierarchical process that involves a series of innate and learned behavioral decisions made by an animal, based on what habitat it would use at different environmental scales' (Hutto 1985; Krausman 1999, p. 86).

Microhabitat selection may have major consequences for the biology of an organism, since it determines the environmental conditions under which it can survive and reproduce (Sih et al. 1992; Martin 2001; Dias and Machado 2006). Therefore,

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microhabitats are important in determining the local distribution patterns of small animals on a micro scale (Krebs 1972; Cady 1984).

Generalisation of habitat selection in spiders is complicated due to their wide range of foraging strategies (Wise 1993). When selecting suitable habitats these arthropods must take into consideration a number of factors including thermal and structural conditions, water and food availability, predation risk and likelihood of reproductive success (Morse and Stephens 1996; Martin 2001; Goldsbrough et al. 2004). Temperature is a very important factor in microhabitat selection for spiders as, being ectothermic organisms, they are limited by the thermal condition of their environment (Cobb 1994; Voss et al. 2007). This environmental variable is known to affect habitat selection in spiders, mainly through prey availability and the presence of favourable conditions for their growth and reproduction (Riechert and Tracy 1975; Goldsbrough et al. 2004; Glover 2013). In addition, temperature is a relevant variable in microhabitat selection of specialised ectotherms living under rocks, as in the case of some spiders and small vertebrates (Huey 1991; Goldsbrough et al. 2004; Díaz et al. 2006; Van den Berg et al. 2015). The properties of rocks such as colour and size (diameter, length and thickness) can affect the transfer and accumulation of heat from the environment to the spaces underneath the rocks (Huey et al. 1989). Under rocks, spiders will avoid thermal stress and thus maximise their feeding activities by selecting more thermally favourable microenvironments (Riechert 1976). Usually nocturnal ectotherms select larger rocks in the field because in high-temperature conditions thermoregulation is better under these rocks (Huey 1991). Larger rocks retain heat longer and at the same time allow organisms to avoid reaching critical temperatures during the day under thermal stress conditions (Huey et al. 1989).

Studies in cursorial or wandering spiders have shown that temperature and shelter size can play an important role in microhabitat selection, particularly in spiders that live in desert environments (Goldsbrough et al. 2004; Glover 2013; Van den Berg et al. 2015). In fact, spider species that live in thermally stressful environments could be ideal models for understanding how animals use behavioural and physiological strategies to mitigate the probability of encountering thermal extremes (Van den Berg et al. 2015). In South America, there are no studies that evaluate microhabitat selection in desert spiders, or any studies which compare patterns of microhabitat selection among desert-dwelling species around the world. This study will help further our understanding of the factors which influence microhabitat selection in cursorial desert-dwelling spiders, giving us a more complete view of this topic in the Neotropical region.

The family Sicariidae consists of two genera in South America, *Loxosceles* Heineken & Lowe and *Sicarius* Walckenaer (Magalhães et al. 2017). Species of the genus *Sicarius* are known as sand recluse spiders; they live in desert and semi-desert climates and are well known for their peculiar self-burying behaviour (Magalhães et al. 2013). The spider *S. thomisoides* is a nocturnal ectotherm that has a wide distribution in Chile, having been observed from central Chile to the Atacama Desert (Magalhães et al. 2017). The climatic differences found at altitudinal and latitudinal levels in Chile suggest possible local thermal adaptations in this species. In this case, one of the most marked differences in temperature is the contrast between coastal and inland locations, with lower average and maximum temperatures near the coast (diCastri and Hajek 1976).

In this study, we investigated whether individuals of the spider *S. thomisoides*, which are commonly observed under rocks in desert and semi-desert habitats (Taucare-Ríos and

Sielfeld 2013; Magalhães et al. 2017), exhibit microhabitat selection at different locations along their distribution, and whether temperature or rock size are clues for habitat selection. We conducted the analysis at two scales: (1) regionally, comparing habitat selection between coastal locations and inland locations; and (2) locally, comparing the effects of rock size and temperature on habitat selection. We selected coastal and inland locations because locations close to the coast have lower temperatures than locations far from the coast during the summer period. If large-scale climatic conditions are important for this species, spiders may be expected to select lower temperatures on the coast than at the inland locations. In addition, we would expect that this spider would select larger rocks at locations far from the coast, which experience higher temperatures during the day and lower temperatures during the night, while selecting smaller rocks at locations near the coast, which experience lower temperatures.

Materials and methods

Study area

We selected six locations with different climates from the known distribution of *S. thomisoides* in Chile. We defined two classes of macrohabitats – close to the coast (coastal locations) and far from the coast (inland locations) – based on differences in average temperature in January 2016 (obtained from https://es.climate-data.org/). Coastal locations: Iquique (20.126°S, 70.921° W; mean temperature: 21.1°C; max temperature: 25.3°C), Punta de Choros (29.144°S, 71.274°W; mean temperature: 18.6°C; max temperature: 22.5°C) and Maitencillo (32.31°S, 71.270°W; mean temperature: 19.1°C; max temperature: 24.7°C). Inland locations: Canchones (20.255°S, 69.334°W; mean temperature: 22.2°C; max temperature: 28.2°C), Vicuña (30.01°S, 70.42°W; mean temperature: 20°C; max temperature: 25°C) and Lo Prado (33.26°S, 70.43°W; mean temperature: 20.5°C; max temperature: 29.5°C) (Figure 1).

Field work

At each locality, we used 10 × 5 m transects, along which we actively searched for spiders under rocks for about 2 hours/day between 10:00 and 12:00 in January of 2016 (summer). We recorded rock temperature with an infrared thermometer, rock size (length), and the presence/absence of spiders for each rock per transect (Goldsbrough et al. 2004). In addition, we measured air temperature, soil temperature and body temperature (Tb) for each spider, with a non-invasive infrared thermometer (Veloso et al. 2012). All adults and juveniles were captured, measured (carapace width in mm) and sexed following Magalhães et al. (2013). Following this method, adult females were identified by a dense tuft of plumose setae just anterior to their spinnerets, while adult males were identified by the completely developed copulatory organs at the end of their palps.

Analysis

We performed a logistic regression using MINITAB v. 16.0, where the response variable was presence/absence of spider under the rock and the predictor variables were temperature, air temperature, soil temperature and rock size. To evaluate selectivity,

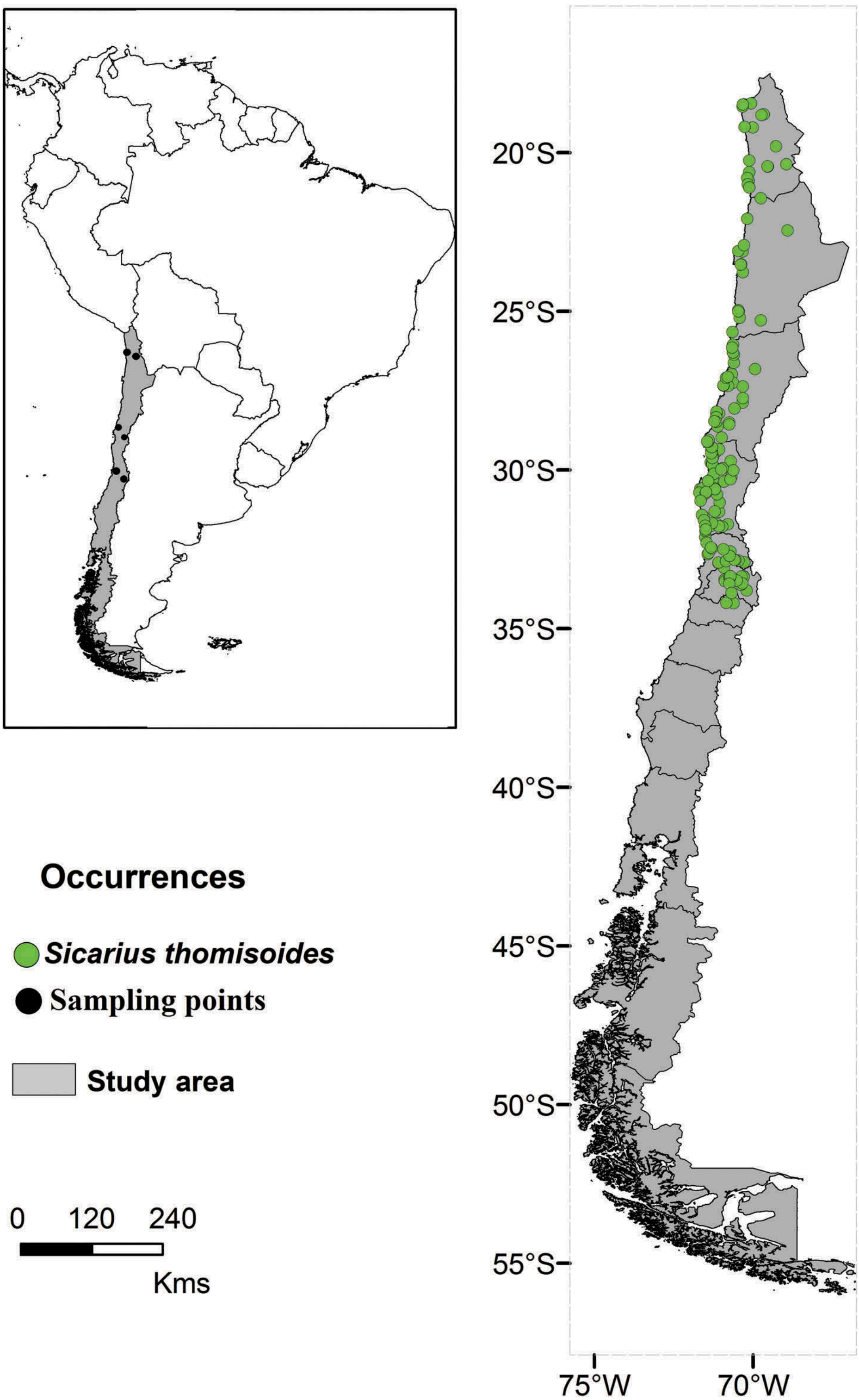

Figure 1. Geographical distribution of S. *thomisoides* and sampling sites selected for the study.

we used the Savage selectivity index, where values above 1 indicate positive selection and those below 1 indicate avoidance (Manly et al. 1993). This index takes into account the number of available rocks vs the number of rocks actually occupied. Rock sizes and temperatures have been grouped arbitrarily into ranges. For rock sizes, the range was: smaller rocks (20–40cm) and larger rocks (above 40 cm). For rock temperatures: cold (15–20°C); medium (21–25°C), warm (26–30°C) and very hot (above 31°C). The degree of selectivity for different sizes and temperatures of rocks for coastal and inland populations were evaluated by factorial analysis of variance (ANOVA). The factors corresponded to macrohabitat (coast vs inland) and rock temperature and rock size chosen. The association between rock temperature and Tb, as well as rock size and carapace width (CW, as a proxy for body size) were tested using Pearson correlation for both coastal and inland populations. We tested the assumption of normality and homoscedasticity with Kolmogorov-Smirnov and Levene, respectively.

Results

We sampled a total of 263 rocks, with 93 rocks having spiders beneath them. The frequency of occupation of the rocks varied from 21.67 to 51.22% among locations. Females and juveniles were most commonly recorded, making up 46.23 and 45.16% of the total number of spiders sampled, respectively. In coastal populations males and females predominated, whereas in inland populations juveniles and females were dominant. Most (occupied) rocks (92.47%) included only one individual while 5.32 and 2.15% of the rocks had two and three individuals per rock, respectively; in the instances where there was more than one spider they were often found eating one another (Figure 2(a–b)). In general, we found that adults tended to occupy large rocks while juveniles were found more commonly under small rocks (Figure 3(a)). Interestingly, we observed higher numbers of juveniles under larger rocks in sites with a lower proportion of adults: Canchones, Lo Prado and Vicuña (Figure 3(b)). We found a positive correlation between the spider body size (CW) and the selected rock size both in coastal ($r = 0.44$, $p = 0.001$, $n = 50$) and inland ($r = 0.58$, $p = 0.001$, $n = 43$) populations.

We found that spiders selected large and warm rocks in all localities, independent of the distance of the locality from the coast (Table 1). The spiders preferred rocks with temperatures between 26 and 30°C (ANOVA, $F_{1,4} = 6.92$, $p < 0.05$) and rocks larger than 40 cm (ANOVA, $F_{1,4} = 4.18$, $p < 0.05$) (Figure 4). Rock selectivity did not differ significantly between macrohabitats (rock temperature: ANOVA, $F_{1,20} = 1.65$, $p = 0.21$; rock size: ANOVA, $F_{1,20} = 0.01$, $p = 0.89$) and we did not find interaction effects between rock temperature selectivity and macrohabitat (ANOVA, $F_{2,20} = 2.79$, $p = 0.06$) or between rock size selectivity and macrohabitat (ANOVA, $F_{2,20} = 1.10$, $p = 0.37$). A significant and positive effect on the probability of finding a spider was found for both rock temperature and rock size, while air temperature and soil temperatures had no significant effect (Table 2). We found a positive and strong relation between rock temperature and Tb both in coastal ($r = 0.58$, $p = 0.0001$, $n = 47$) and inland ($r = 0.67$, $p = 0.0001$, $n = 46$) populations.

Figure 2. (a**)** Adult female of *Sicarius thomisoides* in a typical hunting position under a rock in Punta de Choros. (b) Female eating a conspecific under the same rock in Maitencillo.

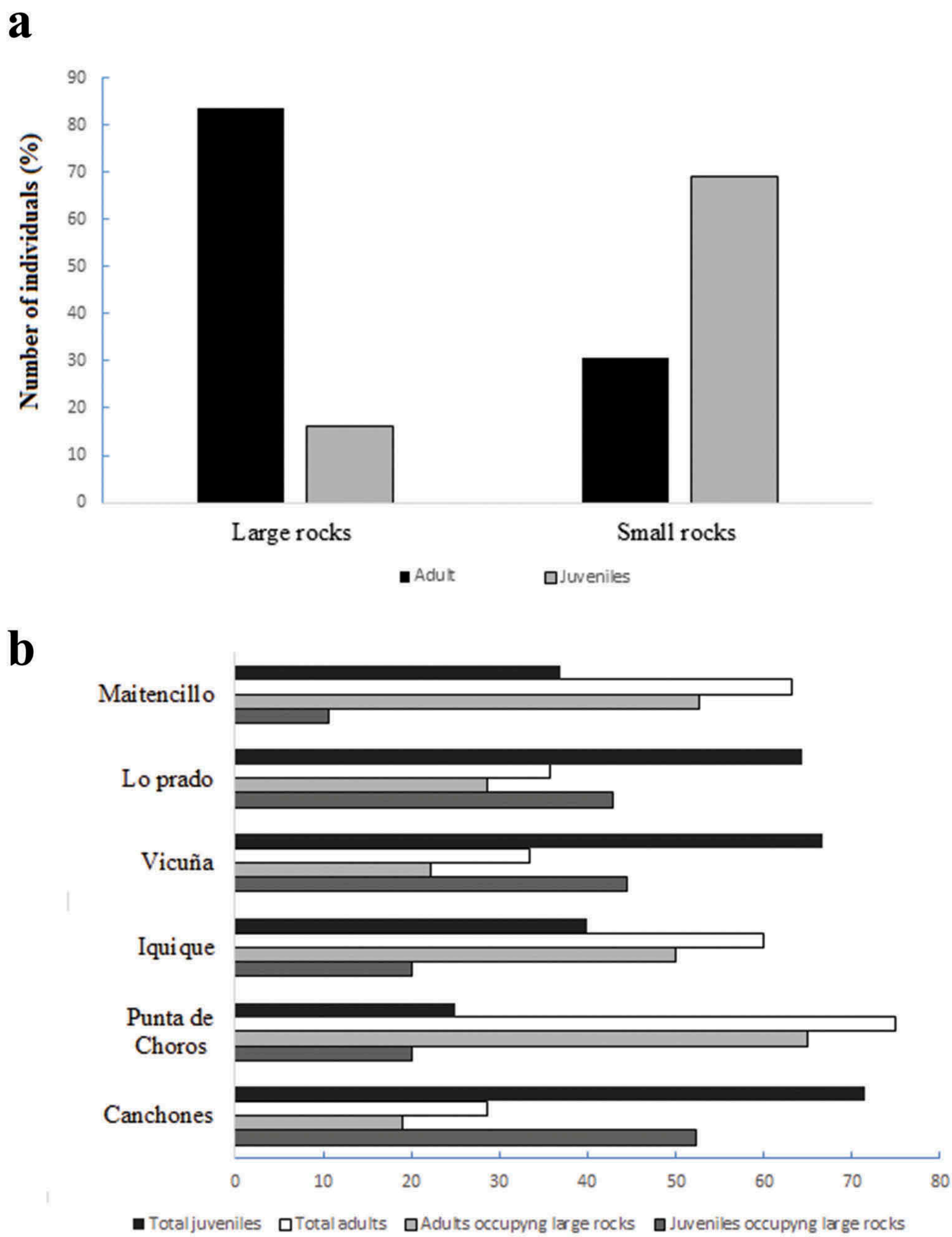

Figure 3. (a) Proportion of individuals found under large and small rocks. Large rocks: larger than 40 cm; Small rocks: smaller than 40 cm. (b) Proportion of juveniles and adults using only large rocks in different locations.

Table 1. Rock sizes and rock temperatures selected by *Sicarius thomisoides* in each locality. The number of adults and juveniles is also included.

Locality	n	Average rock size (cm)	Average rock temperature (°C)	*S. thomisoides*	
				Adults	Juveniles
Iquique	10	48.8	31.21	5	5
Canchones	20	46.81	33.22	6	14
Punta de Choros	21	47.5	25.83	17	4
Vicuña	9	42.45	29.71	3	6
Maitencillo	19	42.5	24.88	12	7
Lo Prado	14	38.5	28.72	5	9

Discussion

The importance of microhabitat selection for ectotherms has been previously emphasised in the literature (Huey 1991; Schlesinger and Shine 1994; Webb and Shine 2000; Sabo 2003; Goldsbrough et al. 2004; Díaz et al. 2006), and some studies show that it has a major impact on the thermal physiology and ecology of these animals (Huey 1991; Goldsbrough et al. 2004; Díaz et al. 2006). Our results indicate a clear microhabitat selection behaviour by the spiders. We found a positive effect of temperature and rock size on the presence of *S. thomisoides*. The spiders positively selected rocks at temperatures between 26–30°C and avoided low (15–20°C) and high temperatures (36–40°C) during the day, and they preferred to take refuge under large rocks, independent of the environmental conditions of the macrohabitat. Similar results have been found in other studies (Sabo 2003; Goldsbrough et al. 2004, 2006; Van den Berg et al. 2015), while selection for large rocks has been found in other ectotherms, both vertebrates and invertebrates (Martin and Salvador 1997; Goldsborough et al. 2004; Díaz et al. 2006).

The lack of differences in selectivity between coastal and inland populations highlights the importance of microenvironments or microclimates in microhabitat selection (Pringle et al. 2003). In this case, microhabitat selection does not appear to be influenced by differences in thermal condition between macrohabitats. Thus, the habitat structure could be important in determining the thermal attributes of retreat sites used by sedentary and/or nocturnal ectotherms (Huey et al. 1989; Kearney 2002; Pringle et al. 2003).

Ectotherms organisms maintain constant Tb by selecting microhabitats that provide environmental temperatures within a narrow optimal range (Huey 1991; Rubio and Carrascal 1994; Sabo 2003). In spiders, the selection of suitable thermal refuges is critical for growth and survival, where the temperature defines foraging and reproduction sites (Morse and Stephens 1996; Goldsbrough et al. 2003, 2004; Glover 2013). In desert climates, shelter can reduce thermal stress and desiccation, enabling spiders to remain cooler during the warmest parts of the day (Lubin and Henchel 1990; Glover 2013). This could be especially important for *S. thomisoides*, affecting its activity in desert environments. Our data suggest that S. *thomisoides* selects warmer rocks in summer, and show that microhabitat selection is not affected by air or soil temperature, which demonstrates a capacity for thermoregulation. We hypothesise that the rock temperatures chosen by spiders in all localities were always below some critical temperature and close to an optimum performance temperature (data not shown, 27.03 ± 3.73°C); this

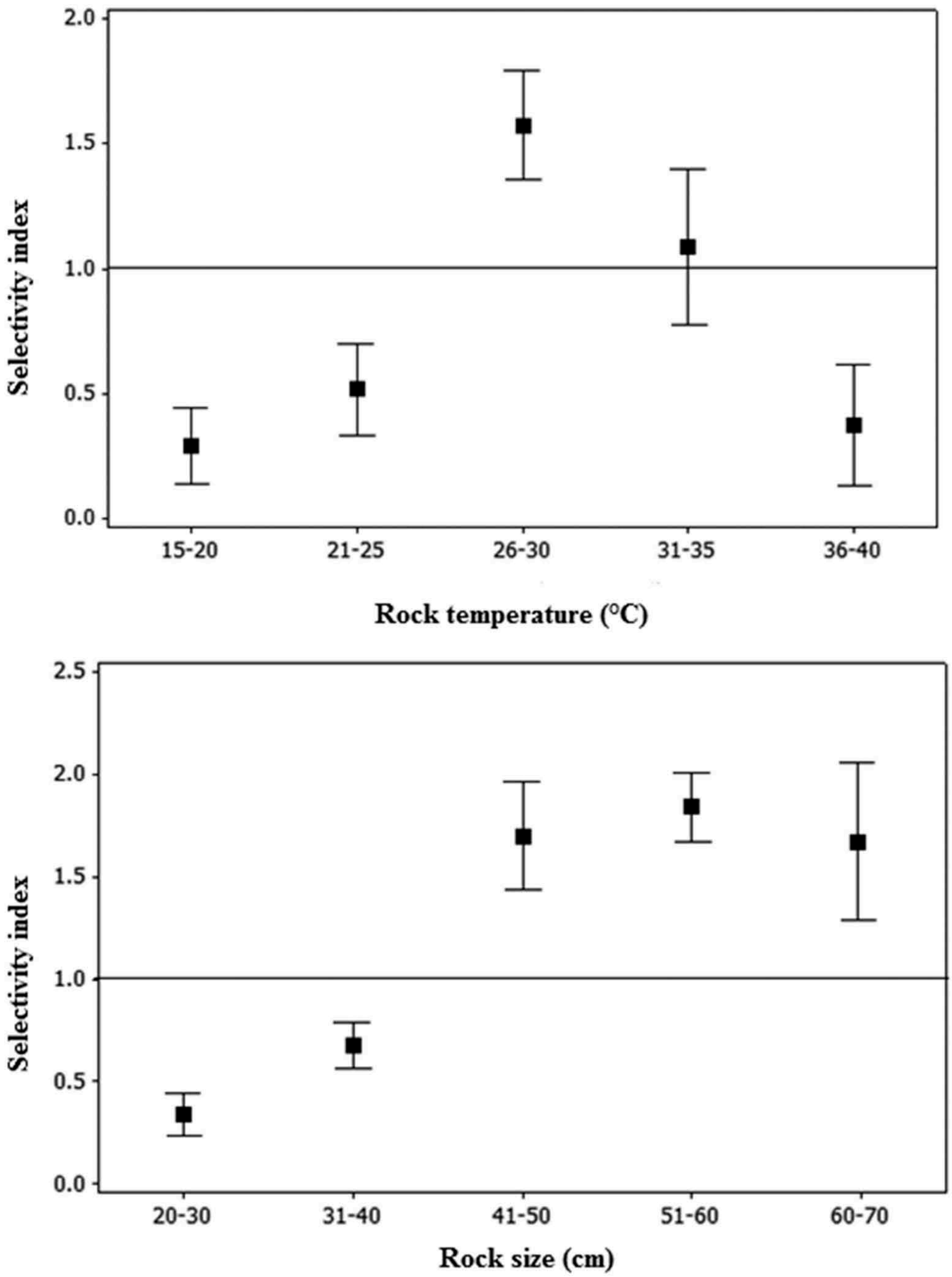

Figure 4. Selectivity of *Sicarius thomisoides* to different rock sizes and rock temperatures. Values above 1 indicate a positive selection; values below 1 indicate rejection or avoidance (mean ± standard deviation).

Table 2. Results of logistic regression for the different variables evaluated.

Parameters	Coefficients	SE	P
Constant	−6.16	1.006	0.0001
Rock size (cm)	0.048	0.012	0.0001
Rock temperature (°C)	0.228	0.045	0.0001
Soil temperature (°C)	−0.051	0.035	0.149
Air temperature (°C)	−0.045	0.025	0.067

corresponds with patterns observed in other organisms living under rocks (Huey et al. 1989; Huey 1991; Sabo 2003).

As stated above, S. *thomisoides* also demonstrated a strong positive selection for large rocks. As with warm rocks, larger rocks provide better opportunities for thermoregulation, but also provide opportunities for water regulation in open areas, decreasing the spiders' probability of encountering extreme upper temperatures (Huey et al. 1989). We cannot assume, however, that the selection for large rocks can be solely explained by the species' thermoregulation needs. Alternatively, S. *thomisoides* may to some degree select larger rocks as part of a predator avoidance strategy, to increase the probability of encountering prey or to reduce the likelihood of being disturbed by large vertebrates (Rubio and Carrascal 1994; Schlesinger and Shine 1994; Díaz et al. 2006; Van den Berg et al. 2015). Thus, the selection of microhabitat in this spider may be a compromise between its ecology and physiological restrictions (Huey and Stevenson 1979; Huey et al. 1989).

On the other hand, the data suggest there is a difference in microhabitat selection between adult and juvenile individuals (Dias and Machado 2006). The fact that most individuals found in this study were alone under rocks suggests that individuals of *S. thomisoides* are intolerant to conspecifics. An interesting hypothesis by Morse (1980) proposed that microhabitat utilisation may not necessarily follow from habitat selection, because if populations are large and resources (in this case rocks) are limited, intra- and interspecific competition can exclude animals from preferred habitat (Glover 2013). In this study, adult spiders were found in greater numbers under large rocks while juvenile spiders were found in greater numbers under small rocks. We suggest that this may not be a result of juvenile spiders preferring small rocks but rather due to adult spiders excluding juveniles from large rocks through competition and cannibalism. This is likely to be the case, as when adult numbers were low there was an increase in numbers of juveniles under large rocks.

The habitat of an organism determines the microclimates available which consequently affects the animal's physiology and ecology (Huey 1991; Van den Berg et al. 2015). In this scenario, diurnal thermoregulation for ectotherms that live in deserts is limited to retreat site selection and their ability to exploit thermal conditions provided by their retreat from the habitat (Kearney and Predavec 2000; Van den Berg et al. 2015). This paper highlights the importance of rock size and rock temperature for microhabitat selection in *S. thomisoides*, and confirms the same pattern found in other spiders that live in habitats with thermally extreme environments (Goldsbrough et al. 2003, 2004; Van den Berg et al. 2015).

In conclusion, our study shows that *S. thomisoides* uses microhabitat selectivity and that it selects warm and large rocks. Adults selected larger rocks than juveniles did, but we suggest this may be a result of juveniles being excluded from larger rocks by adults.

On the other hand, rock selection was not affected by climatic conditions, highlighting the importance of microscale conditions on microhabitat selection in these organisms. Finally, we provide a compelling picture of a spider that actively selects retreat sites according to thermal conditions and rock size. However, we do not know if there are other factors that could better explain rock selection in this species (e.g. prey availability, humidity or predator presence). Future studies should be conducted into these niche variables, assessing the level of influence they have over microhabitat selection for this species.

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Disclosure statement

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