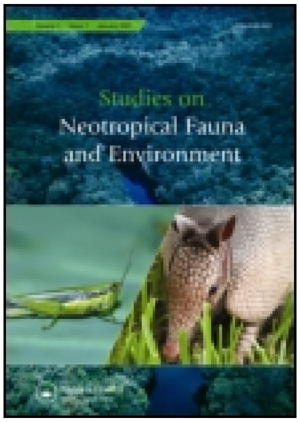

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Spatial distribution, burrow depth and temperature: implications for the sexual strategies in two *Allocosa* wolf spiders

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ORIGINAL ARTICLE

Spatial distribution, burrow depth and temperature: implications for the sexual strategies in two *Allocosa* wolf spiders

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Allocosa brasiliensis and *Allocosa alticeps* are two burrowing wolf spiders that inhabit Uruguayan sandy coasts. Male efficient digging is necessary because copulation and oviposition occur inside their burrows. We examined burrow distribution, density and temperature variation according to burrow depth. Adult burrows were more frequent at the slope of sand-dunes in *A. alticeps* and at the base in *A. brasiliensis*. The base provides better digging conditions, whereas *A. alticeps* adults could prefer the slope to avoid intra-guild predation. Temperature buffering increased with depth, providing thermal stability in such a harsh environment as coastal dunes.

Keywords: burrow spatial distribution; depth; sand dunes; temperature buffering; wolf spider

Introduction

Sandy coastal areas in Uruguay are considered harsh and unpredictable environments characterized by a great seasonal and daily variation in temperature, humidity, winds and solar radiation conditions (Defeo & Martínez 2003; Costa et al. 2006). Animals that inhabit coastal areas will need morphological and behavioral traits to help them face problems such as high temperatures during the day that drop drastically at night, to prevent water loss, and/or to find refuge in areas with scarce vegetation (Gwynne & Watkiss 1975; Cloudsley-Thompson 1982; Gudynas 1989; Henschel 1990; Henschel & Lubin 1992; Christy et al. 2003; Celentano & Defeo 2006). In the case of spiders, such conditions favor the occurrence of burrowing more than aerial web-building spiders, as was reported by Costa et al. (2006) for open dunes in Uruguayan coastal areas.

Allocosa brasiliensis (Petrunkevitch, 1910) and *Allocosa alticeps* (Mello-Leitão, 1944) are sympatric and synchronous wolf spiders that inhabit the sandy coasts of Uruguay (Capocasale 1990; Costa 1995; Costa et al. 2006). Individuals are nocturnal and construct burrows where they stay during daylight and in the coldest months, being especially active during summer nights (Costa 1995; Costa et al. 2006). Male burrows of both species are approximately 10 cm deep, while female and juvenile burrows are shorter (Capocasale 1990; Aisenberg et al. 2007). Previous studies proposed a reversal in sex roles and sexual size dimorphism for both *Allocosa* species (Aisenberg et al. 2007; Aisenberg & Costa 2008). Females are smaller than males and they are the roving sex that locates sexual partners and initiates courtship. Copulation takes place inside the male burrow and after the final dismount, the male leaves and both sexes collaborate in closing the burrow entrance. The female remains inside the male burrow and will lay the egg-sac there. Females leave male burrows after hatchlings' emergence, when it is time for spiderling dispersal (Costa et al. 2006; Postiglioni et al. 2008). On the other hand, as copulation occurs exclusively inside male burrows, males will need to construct another burrow for gaining access to new sexual partners (Aisenberg et al. 2007; Aisenberg & Costa 2008).

According to previous studies, female mate choice is based on burrow length in both *Allocosa* species (Aisenberg et al. 2007; Aisenberg & Costa 2008), so strong selection on burrow quality – stability, adequate temperature and humidity conditions – could be expected. Furthermore, the larger size of males compared to females could be associated with male–male competition for access to territories where they can construct more stable and deeper burrows. The objectives of the present study were to examine burrow density and its distribution along the sand-dune profile, and to determine if burrow depth is related with temperature buffering in both *Allocosa* species. Additionally, we collected data of nocturnal surface activity on the sand surface, distinguishing the individuals according to sex and species. The present study

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may provide insight to the constraints shaping burrow construction in *A. brasiliensis* and *A. alticeps*, generating hypotheses on the cost of burrowing and its consequences for the sexual strategies shown by each species.

Materials and methods

Burrow spatial distribution and surface activity

We performed five monthly samplings between November 2007 and March 2008 in the coastal sand dunes of Marindia (34°46′52.3″S, 55°49′51.5″W), Canelones, Uruguay, 60–70 m north from the wave break-point. The study was carried out during one whole reproductive period of *Allocosa* (Costa et al. 2006; Aisenberg & Costa 2008). Sifting samplings were performed by four collectors during day-light in square plots of 1 m^2. We drew two plots on the sea-side and two on the land-side, drawn parallel to the line of the coast on the first line of dunes. The working area was characterized by the presence of open sand dunes, without trees or shrubs and with disperse *Panicum racemosum* (Gramineae), *Hydrocotyle bonariensis* (Umbelliferae) and *Senecio crassiflorus* (Compositae) as predominant vegetation (Costa 1995). Spiders were collected by sifting the sand of each plot down to 20 cm depth, using geological sieves with a mesh size of 4 mm. The four collectors worked simultaneously on each plot and registered the location of all *Allocosa* spp. individuals.

We also performed nocturnal manual captures during the same period in areas along the coastline approximately 200 m away from the places that had been chosen for day-light samplings. After sunset and during 1 h, three to six researchers using headlamps collected *Allocosa* spiders walking. All the individuals were carried to the laboratory for identification.

We took sand samples of the surface of four different areas (sea-side base, sea-side slope, land-side base, land-side slope) of one randomly chosen dune. We performed granulometric analyses of each sample at the Departamento de Evolución de Cuencas, Facultad de Ciencias, Montevideo, Uruguay.

Temperature versus burrow length

Ninety-eight burrows of *A. brasiliensis* and *A. alticeps* were recorded in the first line of dunes in Lagomar, Canelones, Uruguay (34°50′59″S, 55°58′35″W) between August 2004 and April 2005. Temperatures inside the burrow were recorded once at the bottom of each burrow, using a digital thermocouple Digi-Sense, Cole Parmer. The air temperature was registered approximately 5 cm away from the burrow entrance and 10 cm away from the surface. We measured burrow depth in all the cases. Measurements were performed by two researchers for 1 h after sunset, when *Allocosa* spiders present higher surface activity and burrows are open (Costa 1995).

Statistical analyses

The results were analyzed using PAST: Palaeontological Statistics version 1.8 (Hammer et al. 2004) and WINPEPI version 9.4 (Abramson 2004). For comparisons between both collecting methods we divided the number of collected spiders per the number of collectors. Frequencies were compared using the Chi square test for independent samples and Fisher's exact test. We used Student's *t*-tests to compare temperatures inside and outside the burrows. We tested for a relation between temperature and burrow depth by using linear regression analysis. We deposited voucher specimens of both species in the arachnological collection of Sección Entomología, Facultad de Ciencias, Montevideo, Uruguay.

Results

Burrow spatial distribution and surface activity according to sex and species

In the nocturnal manual captures we found 78 females and 17 males of *A. alticeps*, and 33 females and 36 males of *A. brasiliensis* (Figure 1). Males represented 18% of total captures in *A. alticeps* and 52% in *A. brasiliensis*. During the sifting sampling we found two females and four males of *A. alticeps*, and four females and two males of *A. brasiliensis* (Table 1). When we divided the number of collected spiders per the number of collectors, nocturnal manual capture was a more efficient method for capturing *Allocosa* individuals than sifting, representing 91% of the captures of adults for both species (Figure 1).

We did not find significant differences in the distribution of *A. alticeps* or *A. brasiliensis* in the land-side or sea-side when we considered the total number of spiders ($\chi^2 = 0.22$, $P = 0.64$). We also compared the distribution of juveniles, males and females of each species in the land-side and sea-side and we did not find differences either for *A. alticeps* ($\chi^2 = 0.55$, df $= 2$, $P = 0.76$), or *A. brasiliensis* ($\chi^2 = 1.99$, df $= 2$, $P = 0.37$).

When we compared the distribution of *Allocosa* individuals found by the sifting method in the base and slope of the dune, we found significant differences in the distribution of *A. alticeps* ($\chi^2 = 6.88$, df $= 2$, $P = 0.03$) but not *A. brasiliensis* individuals ($\chi^2 = 4.92$, df $= 2$, $P = 0.09$) (Table 1). Juveniles of *A. alticeps* were more frequently found at the base of the dunes than females ($\chi^2 = 4.03$, $P = 0.04$)

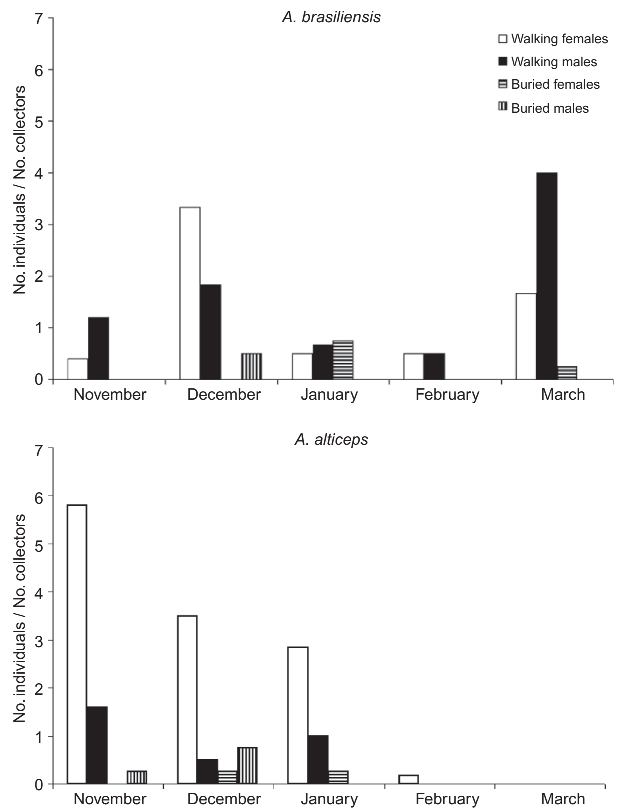

Figure 1. Comparison between the number of individuals per collector of *Allocosa brasiliensis* and *A. alticeps* gathered by hand capture and sifting along the reproductive period.

Table 1. Number of individuals of *Allocosa brasiliensis* and *A. alticeps* found during the sifting, distinguishing between land-side/sea-side and base/slope of the dune.

	A. brasiliensis			*A. alticeps*		
	Juveniles	Males	Females	Juveniles	Males	Females
Land-side						
Base	9	1	3	29	0	0
Slope	11	1	0	14	2	1
Sea-side						
Base	6	0	1	16	1	0
Slope	10	0	0	7	1	1

and adults (females + males) ($\chi^2 = 6.33$, $P = 0.01$), but not males ($\chi^2 = 3.12$, $P = 0.08$). Males and females were more frequent on the slope and did not show significant differences in their distribution (Fisher, $P = 0.67$). When we compared the location of individuals between species, juveniles of *A. alticeps* were more frequent at the base of the dune and juveniles of *A. brasiliensis* were more frequent on the slope ($\chi^2 = 6.76$, $P = 0.01$). Adults of both species showed differences in the location of their burrows: *A. alticeps* adults were more frequent on the slope and *A. brasiliensis* on the base (Fisher, $P = 0.04$) (Table 1). In three cases in *A. alticeps* we found inhabited male burrows separated from inhabited female burrows – one with an egg-sac – by a distance of less than 10 cm.

Table 2. Proportions (in %) of the granulometric fractions of the dune soil samples at Marindia, Uruguay.

	Sea-side base	Sea-side slope	Land-side slope	Land-side base
Coarse sand grains	0.03	0.05	0.04	0.09
Medium sand grains	53.34	55.57	71.85	61.86
Fine sand grains	45.61	43.10	27.69	37.11
Very fine sand grains	0.80	0.86	0.37	0.74
Silt and clay	0.01	0.01	0.00	0.02

The fraction medium sand grain was the most abundant in all the samples (Table 2). The highest difference (18%) occurred regarding this fraction and between the samples from base sea-side and slope land-side. The second most important granulometric component was fine sand grains and the highest difference in composition (17.9%) was also between base sea-side and slope land-side samples. No statistical comparisons were performed due to the few samples.

Temperature versus burrow length

Mean temperatures were 17.5°C ± 2.4 (range 13.8–20.6) outside the burrows and 20.6°C ± 3.6 (range 13.2–27.0) inside the burrows. The average temperature outside the burrow was lower than inside the burrow ($t_{97} = 16.83$, $P < 0.001$; Figure 2). Burrow depth averaged 58.9 mm ± 2.7 (range 9.4–15.5). The differences between the temperatures inside and outside the burrows increased with depth ($R = 0.76$, $F_{3,94} = 43.38$, $P < 0.0001$; Figure 3).

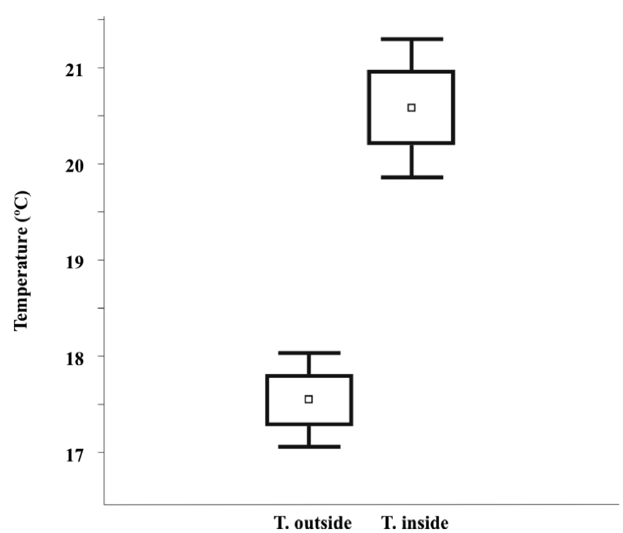

Figure 2. Comparison of mean temperatures inside and outside the burrows of *Allocosa brasiliensis* and *A. alticeps* in the sand dunes at Marindia, Uruguay.

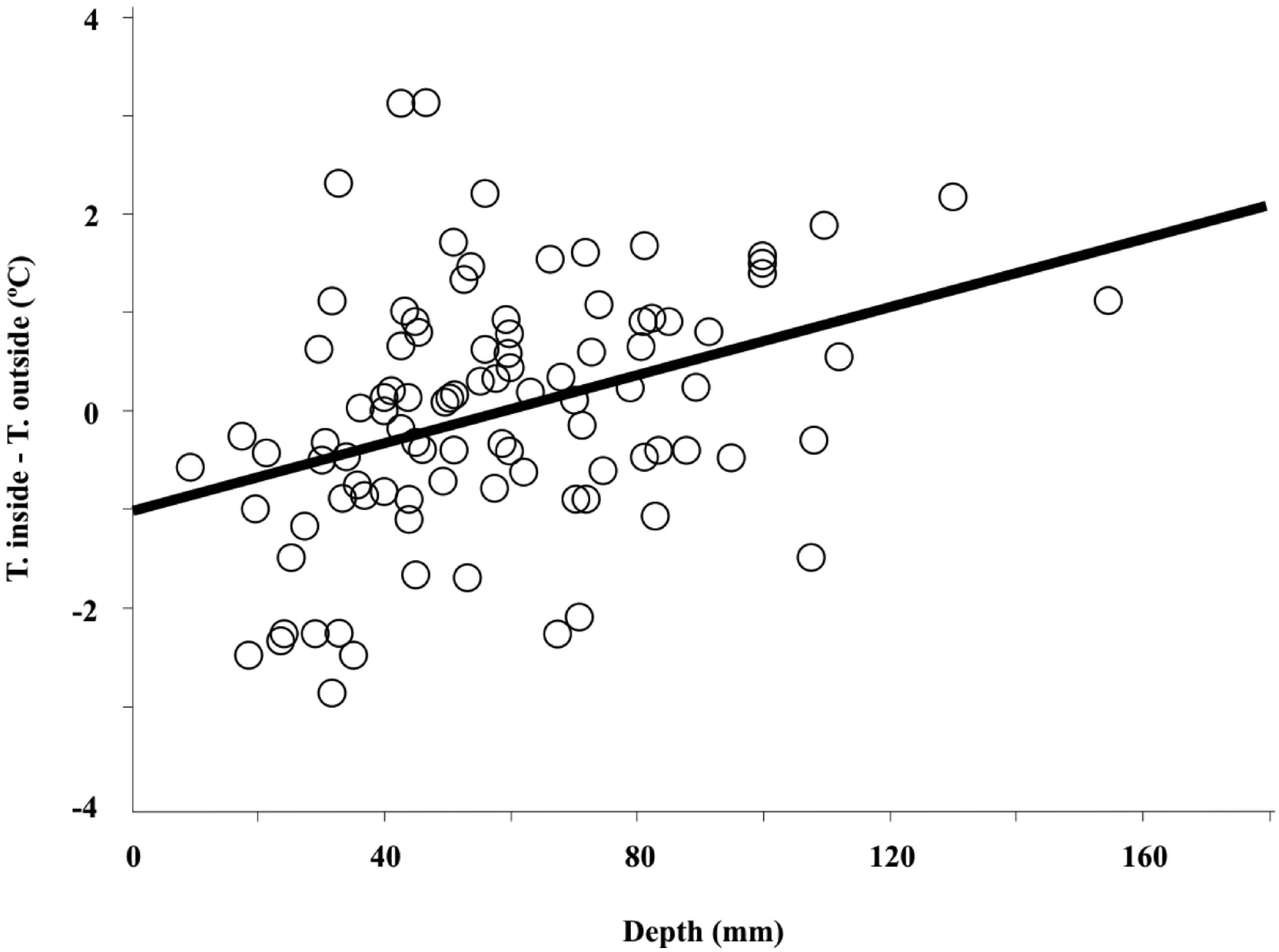

Figure 3. Correlation analysis showing the relation between the difference of temperature inside and outside the burrows of *Allocosa brasiliensis* and *A. alticeps* and burrow depth in the sand dunes at Marindia, Uruguay.

Discussion

Burrow spatial distribution and surface activity according to sex and species

The results confirm that *A. brasiliensis* and *A. alticeps* burrows are clustered differently along the sand dune depending on the developmental stage and species. Preferential areas for digging in adults seem to be the base of the dune in *A. brasiliensis* and the slope in *A. alticeps*. Adults are expected to be more selective when choosing the burrowing sites compared to juveniles. Females prefer to mate with males that have longer burrows (Aisenberg et al. 2007; Aisenberg & Costa 2008), so males will be selected to construct long and stable burrows. Oviposition will take place inside male burrows (Aisenberg et al. 2007; Aisenberg & Costa 2008). The preference of *A. brasiliensis* adults for the base of the sand dune could be associated with better protection from the southwest winds that frequently blow in these areas (Costa et al. 2006; Aisenberg et al. 2009) and, possibly, higher prey abundance (Aisenberg, unpublished data). Individuals of both *Allocosa* species are drastically constrained by humidity levels in the air and in the ground for constructing more stable burrows and for their physiological requirements (Aisenberg, unpublished data). Digging in the sand has been cited as a costly activity for spiders, not only in terms of the energetic cost of digging *per se* but also because of the numerous layers of silk that are needed for providing stability to the burrows (Henschel & Lubin 1992). At the base of the dune high ground humidity levels are reached nearer the surface (Aisenberg, unpublished data), diminishing the energetic costs of digging and maintaining deeper burrows. However, due to small sample sizes, these hypotheses require further testing.

On the other hand, the location of *A. alticeps* adults in the slope could be interpreted as a mechanism to avoid predation by *A. brasiliensis* adults. High levels of intraguild predation have been reported for wolf spiders in general (Fernández-Montraveta & Ortega 1990; Wagner & Wise 1996; Moya-Laraño et al. 2002; Wise 2006), and seem to be common between the two *Allocosa* species (Aisenberg et al. 2009). The larger size and consequently higher predator capacity of *A. brasiliensis* adults seems to be driving the spatial exclusion of *A. alticeps* females and males from the former species' burrowing areas. Territorial exclusion as a mechanism to avoid predation has been suggested for spiders such as *Lycosa carbonelli* and *L. thorelli*, one pair of sympatric wolf spider species (Costa et al. 2000) and between members of the same species in *L. tarantula* (Moya-Laraño et al. 2002), *Agelenopsis aperta* (Riechert 1981), and *Leucorchestris arenicola* (Henschel 1990, 1994).

In both *Allocosa* species, female and male burrows were located on the same sides of the dune, and in *A. alticeps* we found male burrows surrounded by female burrows. These results could be in agreement with the hypothesis of territorial males defending female harems, as has been cited for other arthropods (Eberhard 1975; Fujisaki 1981; Gwynne & Morris 1983; Mora 1990; Buzatto & Machado 2008). Males deliver their burrows to females after copulation and need to dig new burrows to gain more mating opportunities (Aisenberg et al. 2007; Aisenberg & Costa 2008). However, we do not know if males persist on the same areas of the dune after copulation, or just leave and search for a new place for digging. Further research tracking marked individuals at the field will provide insights on these topics.

The higher numbers of *A. alticeps* individuals recorded during our nocturnal samplings and siftings in comparison to *A. brasiliensis* coincides with results from pit-fall traps placed in similar areas (Costa 1995; Costa et al. 2006). We can hypothesize that *A. alticeps* is the more abundant species and/or that individuals of this species are more mobile and, consequently, are more easily collected by either hand capture or pit-fall trap methods. Results also suggest a severe female-biased sex ratio in *A. alticeps* that coincides with brood-rearing experiments under laboratory conditions (Aisenberg & Costa 2008). Further studies will target the confirmation of this bias in the sexual proportion that, if confirmed, has strong implications for the sexual strategies of the species.

Differences in the granulometric composition of the base and the slope of the dune agree with the hypothesis that physical properties of the soil could also be related with differences in the localization between these two species. More data are required to understand if the spatial distribution of *Allocosa* individuals is affected by sand dune dynamics, size and type of sand grains.

Temperature versus burrow length

The positive correlation between temperature and burrow depth, in addition to the differences observed between the temperatures inside and outside the burrows of *Allocosa* individuals, suggest that these refuges provide thermal buffering against the highly variable environmental conditions. Males would be selected to provide burrows with temperature and humidity conditions that allow successful development of eggs and embryos and female survival. Temperature is considered a determinant factor of egg and hatchling development in insects (Wigglesworth 1967) and spiders (Schaefer 1987; Li & Jackson 1996).

According to the present results, larger burrows provide a better temperature buffering that would help individuals, and most importantly egg-laying females, to face the drastic environmental thermo changes of coastal areas. These facts could be driving female mating preference for those males possessing longer burrows, described for both *Allocosa* species (Aisenberg et al. 2007; Aisenberg & Costa 2008).

Future studies will focus on recording humidity conditions inside the burrows, comparing juvenile, female and male burrow characteristics, and sampling on the second and subsequent lines of dunes where vegetation is more abundant, and dune dynamics show differences from the present study site. Finally, we would like to highlight the importance of studying other species of Uruguayan coastal areas to determine divergences and convergences in adaptive solutions in response to environmental pressures, and its implications on the mating strategies.

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