

Male burrow digging in a sex role-reversed spider inhabiting water-margin environments

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Summary

Allocosa brasiliensis is a sex role-reversed wolf spider that inhabits sandy water-margin environments. Males are larger than females and they dig deep burrows, whereas females construct shallow silk capsules. Females are the mobile sex that initiates courtship. Copulations occur inside male burrows and females prefer to copulate with males that construct deep burrows, suggesting high selective pressures acting on male digging behaviour. Our aim was to describe male digging behaviour and burrow architecture in *A. brasiliensis*. We recorded burrow construction of 10 males under laboratory conditions. Male burrows were vertical and tubular, with only one entrance, and in four cases showed a bowl-shaped chamber lateral to the bottom of the burrow. We distinguished eight behaviours associated with burrow construction. We found high frequencies of occurrence of sand extraction and high duration of silk deposition. Burrow characteristics are discussed in the light of the sexual strategies and habitat characteristics of the species.

Introduction

In sandy open habitats with scarce refuges, spiders must prevent water loss and avoid strong winds, extreme temperatures and predators (Cloudsley-Thompson 1982; Henschel 1990). One way of facing high temperatures and desiccation in inhabitants of these harsh ecosystems is to burrow into the sand during daylight hours and restrict the activities outside the burrow to nocturnal hours (Cloudsley-Thompson 1979, 1982). Burrow digging in the sand has been reported as an expensive activity for spiders, mainly due to the production and deposition of silk necessary to maintain stable burrows in that medium (Prestwich 1977; Henschel & Lubin 1992; Craig 2003).

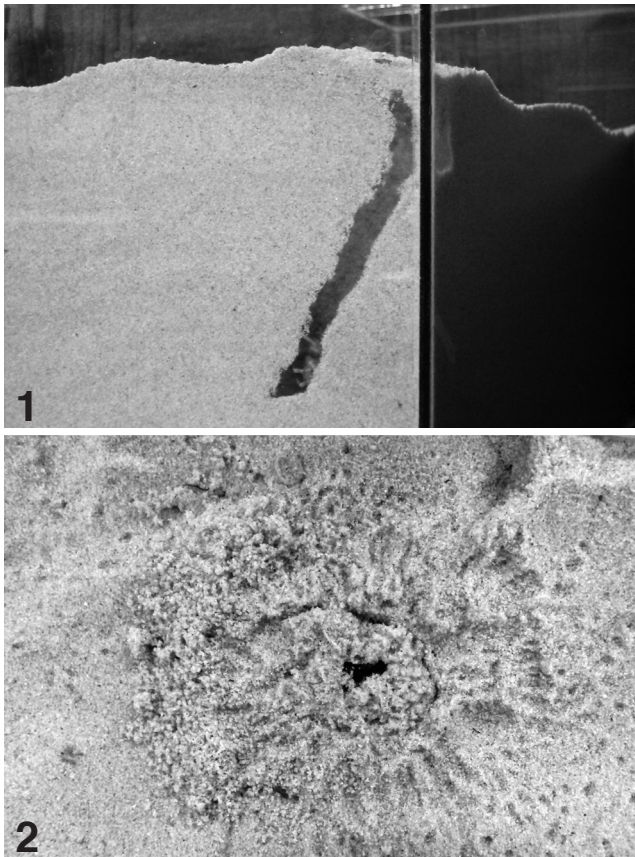
Allocosa brasiliensis (Petrunkevitch 1910) is a wolf spider that inhabits the sandy water-margin environments of South American rivers, lakes and the Atlantic Ocean coastline (Capocasale 1990; Costa *et al.* 2006). This species shows a reversal in typical sex roles and sexual size dimorphism expected for spiders (Aisenberg *et al.* 2007; Aisenberg & Costa 2008). Males are larger than females and they dig deep burrows, whereas females construct silk capsules where they remain during the daytime (Aisenberg *et al.* 2007). The reproductive period takes place during summer of the Southern hemisphere (Costa 1995). Females are the mobile sex that locates male burrows and initiates courtship. Females prefer to copulate with those males that have longer burrows (Aisenberg *et al.* 2007). Copulation

takes place inside male burrows and when it finishes, males exit their burrows and both sexes collaborate in closing the burrow entrance. After the burrow entrance is completely closed, the male leaves and the female stays inside (Aisenberg *et al.* 2007). According to preliminary observations (A. Aisenberg, unpublished data) and pit-fall trap data (Costa 1995; Costa *et al.* 2006), females oviposit inside the male burrow and exit the burrow after spiderlings emerge from the eggsac, with the spiderlings climbing on their dorsum (Aisenberg *et al.* 2007; Aisenberg & Costa 2008). Males of *A. brasiliensis* are expected to have high selective pressures to construct long and stable burrows because those burrows are preferred by females, they serve as mating refuges and will be the nests for the future progeny (Aisenberg *et al.* 2007; Aisenberg & Costa 2008). Recent studies have described specialized setae on the distal section of the male pedipalp that would aid digging function in this sex (Aisenberg *et al.* 2010). Capocasale (1990) gave a brief description of digging behaviour in *A. brasiliensis*; however, no detailed description of this behaviour is available. The objective of this study was to describe digging behaviour in males of *A. brasiliensis* and relate burrow characteristics and digging behaviour to the reproductive strategies of the species.

Methods

We collected 10 adult males of *A. brasiliensis* between January and March 2 in the coastal area of Marindia (34°46'52.3"S, 55°49'29.6"W), Canelones, Uruguay. Spiders were captured by hand during the night using headlamps. The individuals were individually housed in Petri dishes of 9.5 cm diameter and 1.5 cm tall, with sand as the medium and cotton soaked in water. The temperature during breeding was $25.8 \pm 1.0^\circ\text{C}$ (range 24.3–27.5°C). Spiders were fed three times a week with *Tenebrio* sp. larvae (Coleoptera; Tenebrionidae) and small *Blaptica dubia* (Blattaria, Blaberidae). Voucher specimens were deposited in the arachnological collection of the Sección Entomología of Facultad de Ciencias, Montevideo, Uruguay.

One week after their capture in the field, each male was placed into a glass experimental cage 30 cm long, 16 cm wide and 20 cm tall, with a layer of 15 cm of sand as the medium and cotton soaked in water. We moistened the first 5 cm layer of sand placed at the base of the experimental cage. The observations took place between 11 January and 14 March 2009. Preliminary observations (A. Aisenberg, unpublished data) showed that *A. brasiliensis* individuals initiate digging behaviour immediately when they are exposed to daylight. Males were placed in the experimental cages between 2 and 5 pm to motivate fast burrow construction. We recorded burrow construction of 10 males of *A. brasiliensis* during one hour, from the time we detected the occurrence of the first sand extraction behaviour. For detailed analysis, we recorded all the observations with a Sony DCR-SR85 video camera. We analysed the number of occurrences, sequences and durations of behaviours using JWatcher (Blumstein *et al.* 2000).



Figs.1–2: **1** Experimental cage showing an example of male burrow with the spider inside; **2** Example of closed burrow entrance, as seen from above; note the traces left by male foreleg tarsi when closing the burrow entrance from the inside.

Results

Male burrow depth averaged 6.88 ± 2.92 cm, and burrow width averaged 1.30 ± 0.15 cm. The burrows were tubular and vertical, or slightly inclined, with only one entrance (Fig. 1). In four cases, we observed a bowl-shaped chamber of approximately 2 cm in diameter, lateral to the bottom of the burrow. We distinguished eight behaviours associated with burrow construction: sand extraction, exiting the burrow, entering the burrow, silk deposition on burrow walls, silk deposition at the burrow entrance, turning (measured in degrees), blocking the burrow entrance, and resting. Burrow digging began with sand extraction, using chelicerae, pedipalps and occasionally foreleg tibiae, metatarsi and tarsi. Once the hole was excavated, the spider entered and extracted sand from inside the burrow using chelicerae, pedipalps and forelegs. Males frequently left the burrow, deposited sand outside the burrow, and entered again (Fig. 2). This pattern was repeated numerous times during each observation. Males combined sand extraction with silk deposition on internal walls and bottom of the burrow, while turning inside the burrow and depositing silk around the burrow entrance. Finally, the individuals in all cases blocked the burrow entrances by extending forelegs and pedipalps and projecting them to the outside to drag sand towards the entrance. They combined this behaviour with silk deposition around the burrow entrance. Digging concluded with the burrow entrance completely blocked

with a plug composed of silk and sand (Fig. 2). We found a high number of occurrences of extracting sand, entering and exiting the burrow, and a high duration of depositing silk on walls (Fig. 3). Most behaviour durations showed high standard deviation values. In Fig. 4 we show the flow diagram with the mean number of transitions between each behaviour. Again, we highlight the strong interaction among the units corresponding to extracting sand, entering and exiting burrows.

Discussion

Burrow digging by *A. brasiliensis* males comprised high frequencies of occurrence of sand extraction and high duration of occurrence of silk deposition on burrow walls. Sand extraction was similar to the “pulling” described for ant burrowing behaviour as both implied the extraction of the material using mouth parts and forelegs (Halfen & Hasiotis 2010). We did not observe “forcing”, a behaviour described for other burrowing arthropods (Halfen & Hasiotis 2010), that implies pushing material into place with extreme effort as a mechanism to create soil aggregates to stabilize walls and prevent burrow collapse. On the other hand, in this case we found high duration of silk deposition. The deposition of multiple layers of silk during burrow construction has been described for other wolf spiders (Gwynne & Watkiss 1975; Henschel 1990) and probably is necessary to maintain a stable burrow in the sandy habitat where *A. brasiliensis* is found. The numerous movements related to entering and exiting the burrow and extracting sand to the outside could

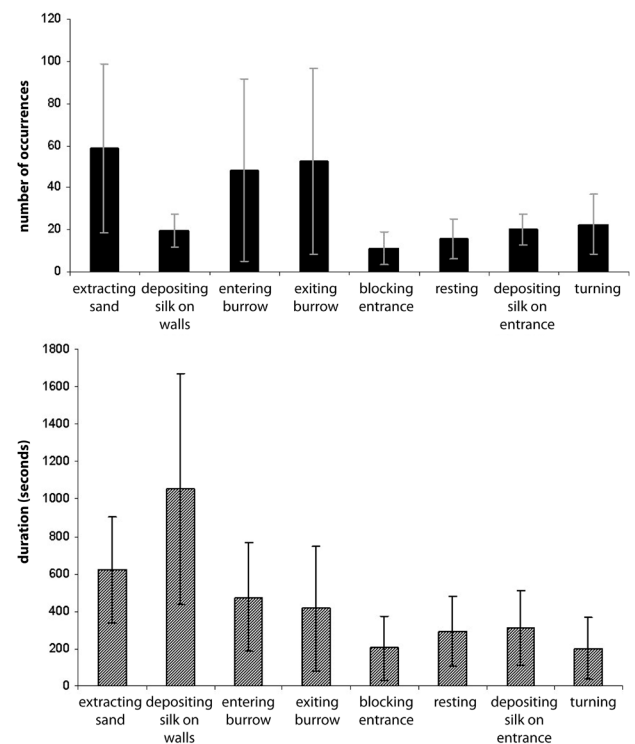


Fig. 3: Mean values and standard deviations of the number of occurrences of extracting sand, depositing silk on walls, entering burrow, exiting burrow, blocking entrance, resting, depositing silk on entrance and turning inside the burrow (upper graph) and their corresponding durations (lower graph), during male burrow digging in *A. brasiliensis*.

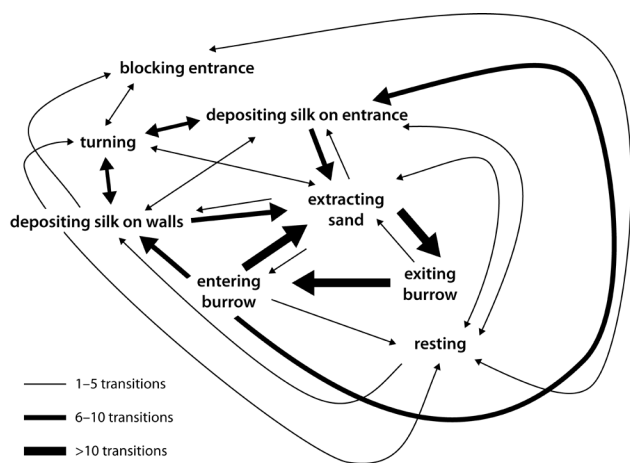


Fig. 4: Flow diagram showing the mean number of transitions for each behaviour described.

increase the risk of predation. However, these behaviours were carried out very quickly, minimizing the exposure of the individuals outside the burrow. The risk of predation on the surface in an open environment is difficult to estimate directly (Henschel & Lubin 1992), so this hypothesis requires further testing.

In the present study, males dug burrows approximately 60% of the length reported for this species in the field (Aisenberg *et al.* 2007). This suggests that the construction of a complete burrow could take several hours. The high standard deviations found in most behaviours that composed burrow digging in *A. brasiliensis* suggest individual variability on male digging performance. This could be expected if we consider that females select their mating partners according to male burrow length (Aisenberg *et al.* 2007; Aisenberg & Costa 2008). Male burrows must be long because this character is selected by females for copulation, but they also need to be wide and stable enough to allow male and female exchange of positions occurring prior to mount, and mount in the typical lycosid position (Foelix 1996). Individual variability of male digging performance and the relation between digging duration and burrow length require further testing. Most wolf spiders copulate outside their burrows, either near the burrow entrance or in the open field (Stratton *et al.* 1996; Dolejš *et al.* 2010). *Allocosa* spiders constitute exceptions to this rule (Aisenberg *et al.* 2007; Aisenberg & Costa 2008), and it would be interesting to investigate the causes of this behaviour. According to Aisenberg *et al.* (2009) and Aisenberg *et al.* (2011), burrow depth in *A. brasiliensis* is positively correlated with temperature buffering and humidity conditions. As these burrows are the breeding nests where the female oviposits and performs egg-sac care until spiderling emergence (Aisenberg, 2010), male construction of a deep and stable burrow will determine the successful development of his progeny. The tubular burrows of *A. brasiliensis* showed in some cases terminal chambers similar to those described for the theraphosid spider *Eupalaestrus weijenberghi* (Thorell, 1894) (Pérez-Miles *et al.* 2005). In *E. weijenberghi* the terminal chamber functions as a defensive mechanism against pompilid wasps (Costa *et al.* 2004). In our case, terminal chambers could also provide protection from *Anoplius* wasps, frequent parasitoids of

this species (Costa 1995; A. Aisenberg, unpublished data). Burrow-blocking behaviours could also help to avoid wasp detection, as well as provide protection from the wind and from sand avalanches, as has been described for *Geolycosa wrightii* (Emerton 1912), another sand-burrowing wolf spider (Gwynne & Watkiss 1975). Future studies will focus on determining the costs associated with burrow digging and estimating the frequency of burrow digging in the field for adult males of this species.

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