Male mate choice in *Allocosa alticeps* (Araneae: Lycosidae), a sand-dwelling spider with sex role reversal

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Abstract. When males have high reproductive investment and female quality is variable, male assessment of sexual partners is expected. *Allocosa alticeps* (Mello-Leitão 1944) is a nocturnal wolf spider that shows a reversal in the sex roles and sexual size dimorphism usual in spiders. Females are the smaller, mobile sex, and they initiate courtship. Males construct burrows that serve as mating refuges and nests for female oviposition and cocoon care. In sex role reversed systems, male mate assessment is expected. Our objective was to test the occurrence of sequential male mate assessment based on female reproductive status and/or body characteristics in *A. alticeps*, discussing the results under sex role reversal hypotheses. We exposed males consecutively to virgin females and mated females and then recorded both courtship performance and mating occurrences relative to individuals' body characteristics. Virgin and mated females detected and entered male burrows in all the cases, and they were courted by males. However, copulations were more frequent with virgin females. The results suggest male mate selectivity in *A. alticeps* is based on female reproductive status. We discuss possible mechanisms underlying male mate choice in this species.

Keywords: Sexual selection, wolf spider, sand dunes, male mate assessment

Traditionally, mate choice studies have focused on female interests, and females are expected to be the exclusively selective sex due to their higher reproductive investment compared to males (Darwin 1871; Andersson 1994). Recent theoretical and empirical evidence shows that when males have high reproductive costs associated with sperm production, mate searching, courtship, copulation, or paternal effort, this sex can also be choosy (Gwynne 1991; Bonduriansky 2001; Clutton-Brock 2007). In sex role reversed systems where male reproductive investment is high and female quality is variable, male mate assessment is expected (Gwynne 1991, 2008; Bonduriansky 2001). Such appears to be the case in the spider *Allocosa alticeps* (Mello-Leitão 1944), a lycosid that shows a reversal in typical sex roles and sexual size dimorphism expected in spiders (Aisenberg & Costa 2008).

Virgin females are expected to provide a higher paternal reproductive success if males are able to monopolize them or minimize female future mating attempts (Carrière & McNeil 1990; Simmons 2001). The preference for virgins over mated females has been reported for several arthropod groups including diverse insects, crayfish, and spiders (Gwynne 1991; Stoltz et al. 2007; Aquiloni & Gherardi 2008). Female fecundity in many arthropods is positively correlated with such traits as body size, weight and body condition (Gwynne 1981; Elwood et al. 1987; Wise & Wagner 1992; Marshall & Gittleman 1994; Uhl et al. 2005), so these variables could also be the target of male mate choice. Most studies report male preference based only on female pheromones (Gasket 2007), but in some cases mate assessment studies include the direct exposure of sexual partners, recording both sexes' responses to all signals exchanged during courtship (Moya-Laraño et al. 2003; Gaskett et al. 2004; Kasumovic et al. 2007; Pruitt & Riechert 2009; Schulte et al. 2010).

Allocosa alticeps is a sex role-reversed nocturnal wolf spider that constructs burrows along the sandy coasts of Uruguay (Aisenberg & Costa 2008). Males are larger than females, and females are the mobile sex that roves searching for males and initiates courtship. Males can respond to female courtship and mount them. Copulation always takes place inside the male burrows. Females prefer to copulate with males that inhabit long burrows (Aisenberg & Costa 2008). After copulation ends, the males exit their burrows, seal the entrances with silk and sand, and leave. Females stay inside male burrows where they will oviposit and exit when it is time for spiderling dispersal (Aisenberg & Costa 2008). Females can lay up to four egg-sacs during the reproductive period, and the first one is the largest in number of eggs (Postiglioni et al. 2008). After clutch emergence, the females will exit male burrows for dispersal of the spiderlings that climb on the female dorsa (Costa et al. 2006). As they are not good diggers (Aisenberg et al. 2010), females will need to copulate again to obtain new male burrows for each oviposition event. As copulations take place exclusively inside their burrows (Aisenberg & Costa 2008), males will need a new deep burrow to have new mating opportunities, and they will be exposed to predation until they construct their new refuge before daylight.

According to sex role reversal hypotheses (Gwynne 1991), males of *A. alticeps* could be selective when making mating decisions. Our objective was to test sequential male mate assessment based on female reproductive status and/or body characteristics in *Allocosa alticeps*. In order to test the central prediction of role reversal, male choosiness among females, we tested male response to consecutive presentations of virgin and mated females of differing body conditions (mass and size). We predicted that males would prefer to copulate with virgins compared to mated females, and with those females that showed high weight values, as a way to maximize their reproductive success. We discuss the results under sex role reversal hypotheses.

METHODS

Natural history.—Individuals reported in earlier studies as *Allocosa* sp. (Capocasale 1990; Costa 1995; Costa et al. 2006; Aisenberg & Costa 2008) were later identified as *Allocosa alticeps* (Aisenberg et al. 2009). Carapace width

averages 2.94 ± 0.30 mm in females and 3.28 ± 0.54 mm in males (Aisenberg et al. 2009). Individuals of *A. alticeps* stay in their burrows during the day and become active during summer nights (Costa 1995). While females construct silk capsules where they remain during daytime, males construct deep and vertical tubular burrows with a single entrance (Capocasale 1990; Aisenberg & Costa 2008). Male burrows average 8.4 ± 1.6 cm length, and 0.8 ± 0.1 cm width (Aisenberg & Costa 2008). Males have specialized setae on the distal section of the pedipalp that aid digging in this sex (Aisenberg et al. 2010). Due to the location of mating, a burrow with a single entrance, and the typical burrow dimensions, we would expect sequential but not simultaneous encounters between a male and more than one female.

Capture and housing.—We collected 22 adult males, 15 mated females (10 with egg-sacs, 5 carrying spiderlings) and 25 sub-adult females of *A. alticeps* in the coastal sand beaches of Marindia, Canelones, Uruguay (34°46′49.9″S, 55°49′34.1″W), from November 2007 to March 2008, and from November 2008 to March 2009. We captured the spiders during the night by using headlamps to locate them walking or leaning out from the burrows, or during daylight by sifting the sand. We housed each spider individually in culture dishes (9.5 cm diam., 1.5 cm height), with sand as substrate and cotton wool soaked in water. We fed individuals three times a week with juvenile cockroaches *Blaptica dubia* (Blattaria: Blaberidae) and mealworm larvae *Tenebrio* sp. (Coleoptera: Tenebrionidae). To obtain virgin females, we daily monitored sub-adults and recorded molting occurrence.

Experimental design.—We performed the trials between December 4 (2007) and April 18 (2008), and between January 2 and March 3 (2009). We used individuals of at least 10 days of adult age, or seven days after their capture at the field. When females were collected with egg-sacs or spiderlings, we removed them and waited ten days before using the spiders in a trial. We fed the animals for the last time 48 h prior to the trials, which began at dusk, coinciding with the period of activity described for the species (Costa 1995).

We carried out the trials in glass cages (30 cm length, 16 cm width, 20 cm height), with a layer of 15 cm of sand as substrate and water supply. We randomly chose individuals for each trial. We placed each male in the arena 48 h prior to the trial, allowing burrow construction. Individuals usually construct their burrows against the glass walls (Aisenberg & Costa 2008), allowing observation and recording of their behaviors inside the burrows. Temperature during the trials averaged $24.63 \pm 1.27°$ C (range: 21–26). We exposed consecutively and randomly each of 15 males of *A. alticeps* to two females of different reproductive status (virgins and mated females). We exposed seven males first to virgin females and the other eight first to mated females. The male's second exposure to a female took place 48 h after the first one. We only considered trials in which the female detected the male burrow within an hour. If courtship did not take place, the trial ended after a 30 min period. We considered ''detection'' as the point when the female, after contacting the silk of the burrow entrance, stood still and leaned into the male burrow. We considered ''female courtship'' the moment when the female entered the male burrow and performed sequences of alternative foreleg waving (shaking bouts) (Aisenberg & Costa 2008). The male

sometimes responded by shaking his body and forelegs rhythmically. If courtship occurred but copulation did not take place, the trial ended one hour after placing the female in the arena. If copulation occurred, the trial finished after the male covered the burrow entrance and left. We did not reuse females. We also recorded the occurrence of attacks that resulted in injuries, leg loss, and/or cannibalism.

Since males of *A. alticeps* are difficult to obtain in the field because of their highly sedentary condition (Costa et al. 2006), we worked through two experimental periods. We performed five complete trials, exposing one male to one virgin and one mated female during the first experimental period (2007–2008) and conducted the other ten trials during the second time period (2009). We carried out the trials in darkness and recorded with a Sony DCR-SR85 digital video-camera with night-shot. We analyzed the video recordings with J Watcher software (Blumstein et al. 2000). We measured carapace width, a measurement considered representative of body size in spiders (Eberhard et al. 1998), abdominal width and weight of all individuals immediately before the trials. The index abdominal width/carapace width was considered as representative of body condition, as described by Moya-Laraño et al. (2003) for *Lycosa tarantula*. We deposited voucher specimens in the arachnological collection of Sección Entomología, Facultad de Ciencias, Montevideo, Uruguay.

Statistical analysis.—We analyzed data with Past Paleontological Statistics version 1.18 (Hammer et al. 2003) and WINPEPI version 1.6 (Abramson 2004). We compared frequencies with Fisher's exact probability test or the McNemar test for dependent samples (paired test). We checked for normal distribution (Shapiro-Wilk test) and homogeneity of variances (Levene test) of courtship, copulatory, and body characteristics. As variables did not follow parametric conditions, we used the non-parametric Wilcoxon matched-pairs sign test to compare courtship and copulatory characteristics when males were exposed to virgin and mated females. We also performed statistical comparisons between virgin and mated female body characteristics (carapace width and weight) with the non-parametric Mann-Whitney *U*-test. We performed logistic regressions with mated (yes/no) as the response and female mating status, carapace width and weight as predictors.

RESULTS

In all cases, virgin and mated females detected and entered male burrows. All virgins ($n = 15$), and 14/15 mated females performed courtship behavior (McNemar test: $\chi^2 = 1.37$, $P = 0.87$). Virgin females performed more foreleg waving bouts during courtship than mated females (Table 1). However, we did not find significant differences in foreleg waving bouts per minute between virgin and mated females. All males courted virgin females, and 14/15 males courted mated females (McNemar test: $\chi^2 = 0.25$, $P = 0.62$). We did not find differences in courtship duration, male abdominal vibration bouts, or male abdominal vibration bouts per minute between virgin or mated females, but male leg shaking bouts and male leg shaking bouts per minute were higher when males were exposed to virgins than to mated females (Table 1).

We did not find statistical differences in the number of copulations for virgins (Fisher's test: $P = 0.57$), or mated females (Fisher's test: $P = 0.26$) obtained during the first or

Table 1.—Female and male courtship characteristics (median ± quartile) in trials with virgin females and mated females, and results of the statistical comparisons between these two groups (non-parametric Wilcoxon matched-pairs sign test).

	Virgin females	Mated females	Statistics
Females			
Number of leg shaking bouts	27.00 ± 43.50	10.5 ± 9.00	$n_1 = 15$, $n_2 = 14$, $T = 16.00$, $P = 0.04$
Number of leg shaking bouts/min	12.35 ± 4.19	17.24 ± 16.60	$n_1 = 15$, $n_2 = 14$, $T = 40.00$, $P = 0.70$
Courtship duration (min)	3.07 ± 2.38	0.90 ± 1.35	$n_1 = 15$, $n_2 = 15$, $T = 20.00$, $P = 0.07$
Males			
Number of leg shaking bouts	211.98 ± 249.70	53.27 ± 159.82	$n_1 = 15$, $n_2 = 14$, $T = 9.00$, $P = 0.006$
Number of leg shaking bouts/min	6.09 ± 3.69	1.44 ± 4.55	$n_1 = 15$, $n_2 = 14$, $T = 6.00$, $P = 0.01$
Number of abdominal vibration bouts	109.50 ± 155.28	100.04 ± 96.98	$n_1 = 15$, $n_2 = 14$, $T = 28.00$, $P = 0.12$
Number of abdominal vibration bouts/min	5.87 ± 3.24	4.23 ± 5.23	$n_1 = 15$, $n_2 = 14$, $T = 41.00$, $P = 0.75$
Courtship duration (min)	7.19 ± 7.54	4.27 ± 4.77	$n_1 = 15$, $n_2 = 14$, $T = 34.00$, $P = 0.24$

second experimental period. We obtained ten copulations with virgin females and three copulations with mated females. Of the eight males that were exposed first to virgin females and then to mated females, in seven cases copulation occurred only in the first exposure, and in one case mating also occurred in the second exposure. Of the seven males that were introduced first to mated females, in only one case did the male copulate with the mated female, and no re-mating occurred. In three cases, males that had been exposed to mated females first and copulation had not occurred, copulated with virgin females in their second contact. Three males did not copulate in either their first or second meeting. Copulations with mated females were longer (36.82 ± 6.41 min) than copulations with virgin females (21.82 ± 9.83 min) ($U = 1$, $n_1 = 9$, $n_2 = 3$, $P = 0.03$). One mated female was attacked prior to mounting and was cannibalized by the male inside his burrow. In this case, the female had courted but the male had not responded with courtship behavior.

The multiple logistic regression with mated (yes/no) as response and female mating status, carapace width and weight as predictors ($\chi^2 = 9.90$, $df = 3$, $P = 0.02$) showed that reproductive status ($\chi^2 = 6.25$, $df = 1$, $P = 0.01$), but not carapace width ($\chi^2 = 2.58$, $df = 1$, $P = 0.11$), or weight ($\chi^2 = 1.00$, $df = 1$, $P = 0.32$), predicted whether copulation would occur (Table 2). Virgin females showed higher weight values than mated females (median ± quartile: virgins 0.11 ± 0.02 g; mated females 0.08 ± 0.02 g; $U = 41.5$, $n_1 = n_2 = 15$, $P = 0.006$), but we did not find differences in carapace width between the two groups (median ± quartile: virgins 2.70 ± 0.30 mm; mated females 2.50 ± 0.37 mm;

$U = 100.5$, $n_1 = n_2 = 15$, $P = 0.86$). Male body size or weight did not seem to affect the occurrence of copulation with virgin or mated females ($\chi^2 = 0.87$, $df = 2$, $P = 0.65$; Table 2).

DISCUSSION

The higher frequencies of male leg shaking bouts and leg shaking bouts per minute performed during courtship and the higher number of matings with virgins compared to mated females correlate with the prediction based on sex role reversal hypotheses (Gwynne 1991; Bonduriansky 2001; Clutton-Brock 2007) that males of *A. alticeps* would be choosy when they make mating decisions. Though both virgin and mated females entered male burrows and performed courtship behavior, males were more prone to mount virgin females. According to the results of the present study, males discriminate between virgin and mated females before mounting. This result was not affected by the order in which the males encountered females of different reproductive status.

Male mate preference biased towards virgin females has been reported for several wolf spiders (Rypstra et al. 2003; Roberts & Uetz 2005; Baruffaldi & Costa 2009) and other spider taxa (Herberstein et al. 2002; Andrade & Kasumovic 2005; Schulte et al. 2010). As we stated earlier, virgin females are associated with greater chances of male paternity success in systems with first male sperm priority (Huber 2005). In *A. alticeps*, females stay inside the male burrow after copulation, oviposit there, and remain buried until they exit the burrow with the spiderlings on their dorsa (Costa et al. 2006). Females can lay up to four consecutive egg-sacs, but the first one is the largest (Postiglioni et al. 2008). Consequently, when males of

Table 2.—Female and male body measurements (median ± quartile) distinguishing when mating occurred or did not occur. Sample sizes (n) are shown between parentheses. Weight measurements of two males that copulated with mated females were lost as a result of human error.

	Virgin females		Mated females	
	Mated ($n = 10$)	Did not mate ($n = 5$)	Mated ($n = 3$)	Did not mate ($n = 12$)
Females				
Carapace width (mm)	2.65 ± 0.37	2.80 ± 0.30	2.50 ± 0.10	2.70 ± 0.55
Body condition index	1.55 ± 0.30	1.44 ± 0.20	1.48 ± 0.12	1.07 ± 0.28
Weight (g)	0.10 ± 0.03	0.11 ± 0.02	0.09 ± 0.01	0.08 ± 0.03
Males				
Carapace width (mm)	3.05 ± 0.35	2.70 ± 0.10	2.70 ± 0.10	3.05 ± 0.50
Body condition index	1.00 ± 0.08	1.00 ± 0.22	1.11 ± 0.11	0.98 ± 0.15
Weight (g)	0.11 ± 0.03	0.09 ± 0.03	0.08	0.10 ± 0.05

A. alticeps copulate with virgin females, they will ensure exclusive paternity of the first and largest clutch.

We did not find differences between mated and virgin females in their approach to male burrows or in the occurrence of courtship. Mated females performed fewer leg shaking bouts during courtship compared to virgins, though we did not find differences in leg shaking bouts per minute or female courtship duration. We do not know the basis of male discrimination, but the lower number of female leg shaking bouts in mated females could reflect a higher sexual reluctance that could also affect male sexual responses. Males might detect subtle differences in courtship behavior, or volatile and/or contact pheromones emitted by females of different mating status, or by previous sexual partners. Nevertheless, mated females entered males' burrows and performed courtship behavior, which suggests that females of this reproductive status are sexually receptive.

Interestingly, when copulations with mated females occurred, they were longer than those of virgin females, as occurs in many arthropods (Simmons 2001). This could suggest the occurrence of sperm displacement mechanisms, plug removal, or intensive stimulation to promote female choice, among other mechanisms described for spiders (Elgar 1995; Eberhard 1996; Huber 2005). The results of the logistic regression suggest that female mating status, but not female body characteristics, is the most important criterion on which males base their mating decisions. When we compared weight between virgin and mated females, virgins were heavier. In this case, it does not mean that female reproductive status and female weight are correlated with male mating acceptance. The logistic regression shows that although virgins are heavier than mated females and males prefer virgins, within each category (virgins or mated) males do not prefer those females showing higher weight values. Characteristics that were not controlled, such as male and female age and male reproductive status, could also affect mate choice in *A. alticeps*, as has been described for other spiders (Gaskett et al. 2004; Uetz & Norton 2007).

In *A. alticeps,* sexual cannibalism has never been reported in the field (Aisenberg et al. 2009) and occurred in only one case in the present study in the absence of male courtship and prior to mounting. This spider is sympatric and synchronic with *Allocosa brasiliensis* (Petrunkevitch 1910), another spider that shows sex role and sexual size dimorphism reversal (Aisenberg et al. 2007). However, males of *A. brasiliensis* frequently show sexual cannibalism on females, reported both in field and laboratory conditions (Aisenberg et al. 2009; Aisenberg et al. 2011). In *A. brasiliensis,* attacks frequently occur after courtship by both sexes and during mounting (Aisenberg et al. 2011). Differences regarding the larger body size, greater longevity (Aisenberg & Costa 2008), and possibly higher energetic requirements in *A. brasiliensis* compared to *A. alticeps* could be affecting mating opportunities and modeling the foraging and sexual strategies of each species.

Future studies will test differences in male mate selectivity when males are exposed to mated females captured with egg sacs or with spiderlings on the dorsa and the effects of male age and reproductive history on mate assessment. We will also test under laboratory conditions if hunger levels and potential mating opportunities affect male mate choice and the occurrence of sexual cannibalism in both *Allocosa* species. Finally, studies about female choice in *A. alticeps* will also help us get a complete picture of the behavioral strategies of the species, elucidating the pressures driving the mating system in this sex role reversed wolf spider.

ACKNOWLEDGMENTS

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