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# MALE RESIDENCY AND MATING PATTERNS IN A SUBSOCIAL SPIDER

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**ABSTRACT.** Male mating strategies are often deployed with regard to female maturity and receptivity, possibly in response to sperm utilization patterns on the part of the female. We examined the pattern of male residency with females during the mating period of the subsocial spider *Anelosimus* cf. *jucundus* (Araneae, Theridiidae). We first examined patterns of male cohabitation with naturally occurring penultimate instar and adult females in the field. Males were significantly more likely to be found in association with adult females, rather than with penultimate instar females. Penultimate instar and virgin adult females of known age were then placed into the field and monitored for residency by subsequently marked males. Males were, again, significantly more likely to be found in association with adult females, rather than with penultimate-instar females, although we were unable to determine if this pattern was due to differential arrival or to differential retention of males at adult female web sites. Aspects of *A.* cf. *jucundus* natural history, including duration of male residency and frequency of mating in the field, are provided for the first time. We discuss the patterns of male residency in relation to predictions based on sperm utilization patterns by female *A.* cf. *jucundus* spiders.

**Keywords:** *Anelosimus*, female maturity, male cohabitation, residency, sperm utilization

Male reproductive success is largely determined by the number of mates males are able to access (Bateman 1948; Jones, et al. 2000). In spiders, where males tend to move around in search of females, a male's mating success will depend on his ability to locate females of the appropriate age and reproductive status and to assess potential paternity success once a female has been located. When females mate multiple times, sperm priority patterns should influence male reproductive strategies (Austad 1984; Eberhard et al. 1993). When paternity is biased towards the first male to mate, males should seek out and guard females who are approaching the final molt (Jackson 1980; Christenson & Goist 1979; Austad 1982; Toft 1989; Watson 1990; Dodson & Beck 1993; Eberhard et al. 1993; Bukowski & Christenson 1997; Bukowski et al. 2001; but see Masumoto 1991). In contrast, males should seek out already mature females when paternity is not biased with respect to male mating order (Eberhard et al. 1993; Schneider 1997) or when paternity is biased towards the last male to mate (Uhl 1998; West & Toft 1999). In the latter case, post-copulatory guarding of females is expected. We examined male mate-finding and residency patterns in relation to female maturity in *Anelosimus* cf. *jucundus*, a subsocial spider species in which, for reasons we discuss below, we suspected sperm utilization patterns to be unbiased with respect to male mating order.

*Anelosimus* cf. *jucundus*, a species to be described shortly (I. Agnarsson in press), is relatively common in riparian regions of southern Arizona. Following a period of maternal care, *A.* cf. *jucundus* siblings remain together in their natal nest until close to sexual maturation, communally capturing and feeding on prey. All clutchmates eventually disperse and establish individual webs at relatively short distances from the natal nest (5 cm–5 m, median = 46 cm; Powers & Avilés 2003). Dis-

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persal typically occurs during the ante-penultimate and penultimate stadia (Avilés & Gelsey 1998). Following dispersal, males and females mature in their individual webs. Although both sexes mature during the same stadium (Avilés & Gelsey 1998), males do so on average nine days earlier than their sibling females (Bukowski & Avilés 2002). After maturation, females typically remain in the webs where they matured while males set out in search of females. While the sex ratio in nests prior to dispersal is even, postdispersal sex ratios are significantly female-biased (Avilés & Gelsey 1998).

The patterns of sexual receptivity in *A.* cf. *jucundus* differ for males and females. Males become sexually active within approximately two days following their final molt, while females become sexually receptive an average of ten days following their final molt (Bukowski & Avilés 2002). The probability of a male courting a female appears to increase as the female gets older (Bukowski & Avilés 2002).

Females readily remate under laboratory conditions and males do not release significantly different numbers of sperm to virgin and non-virgin females (Bukowski & Aviles, unpub. data, using methods of Bukowski et al. 2001 to quantify sperm). Given that paternity patterns in spiders largely reflect the numbers of sperm released (Christenson 1990; Bukowski & Christenson 1997; Schneider et al. 2000; Elgar et al. 2000; Bukowski et al. 2001), we predict that *A.* cf. *jucundus* will have a paternity pattern that is unbiased with respect to male mating order. In such a case, males should preferentially seek out adult rather than subadult females. Here we experimentally examine this prediction and present the first natural history data on mating frequency under field conditions in this spider species.

## METHODS

We conducted our studies in Garden Canyon, a riparian area in the Huachuca Mountains of southeastern Arizona (31.51°N, 110.31°W; 1600–2000 m). *Anelosimus* cf. *jucundus* primarily inhabit juniper trees alongside permanent streams in this area (Fig. 1). Our study involved an early phase, in which we censused naturally occurring webs for patterns of male/female cohabitation, and a later, experimental phase, in which we examined male residency patterns in artificially-established subadult and adult females' webs.

**Early census of naturally-occurring webs.**—On 14 and 24 June 2000, we examined naturally occurring, active, post-natal dispersal webs ($n = 293$) for the presence of subadult and adult males and females. We identified new, active webs containing dispersed individuals by the relative lack of debris, smaller size, and presence of recently maintained capture threads. We recorded the instar (immature versus adult) and sexes of all animals in each web.

**Artificially-established webs.**—On 8 and 13 July 2000, we returned to their collection site 27 penultimate-instar females and 54 adult females that had been individually raised in the laboratory. These spiders had been collected as penultimate-instar females one to two weeks earlier, held individually in 125 ml or 30 ml plastic containers, and fed ad libitum on house flies (*Musca domestica*), walnut flies (*Rhagoletis juglandis*), and fruit flies (*Drosophila melanogaster*).

The spiders were returned to a large patch of naturally occurring *A.* cf. *jucundus* webs to ensure the presence of naturally occurring males. We placed individual females in open 125 ml containers, which we attached to branches of juniper trees. We covered each branch with a fine nylon mesh net to encourage web-construction at the selected site and prevent males or predators from visiting until initiation of the observation period (Fig. 2). When the nets were removed 48 hours later, females had usually expanded their webs from the containers to the surrounding vegetation.

Web sites (defined here as the area within approximately ten centimeters of the female's web) were censused every 1–2 hours over a 24 hour period, every other day. Females returned to the field on 8 July were censused over a period of seven days, and females returned to the field on 13 July were censused over a period of three days. During each census, females were recorded as present or absent and the occurrence of mating and male-male physical contact was monitored.

We individually marked all males that appeared at a female's web site ($n = 76$) with water–based acrylic paints so that we could determine their duration of residency, occurrences of mating and relocation distances.

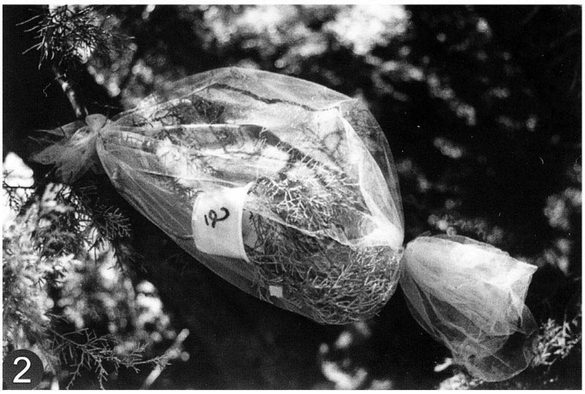


Figure 1.—Juniper trees in the Huachuca Mountains of Arizona, where we artificially established webs of female *A.* cf. *jucundus* spiders in a community of naturally-occurring conspecifics.

Figure 2.—Artificially-established female web site, temporarily surrounded by netting to deter predation or escape as she expanded her web beyond the cup (labeled ‘‘2’’ and attached to a juniper branch).

Figure 3.—Copulation (male on left, female on right).

Figure 4.—Following an extended bout of male-male aggression, this male had tumbled below its combatant, who proceeded to court and mate with the resident female.

First, each unmarked male was removed from a female's web site immediately upon detection or following copulation. Each male was uniquely marked by gently guiding him into a piece of mesh netting and dabbing acrylic paint onto his opisthosoma. Following marking, the male was returned to his place of removal. Most males remained without obvious behavioral long term effects, although six (of 82) males were dropped and lost, and two males were being consumed by female residents during the census following each male's marking.

Matings were defined as pairs in copula with at least one male pedipalp inserted in the female. *Anelosimus* cf. *jucundus* males typically have one insertion with each palp during mating. Matings typically last approximately 135 minutes per pedipalp, with an interim of 35 minutes between pedipalps (Bukowski & Avilés unpub. data). Matings, in light of their lengthy durations, were unlikely to have been undetected during a day of censusing with 1–2 hour inter-census periods.

**Statistical analyses.**—For all maturity analyses, each female was classified as penultimate instar or adult. If seen at a web site during consecutive census periods, a spider was assumed to have remained for the duration between observations. If observed only during a single census period, a spider was considered to have remained for one hour (for duration study purposes). Each adult female web site ($n = 54$) was checked an average of

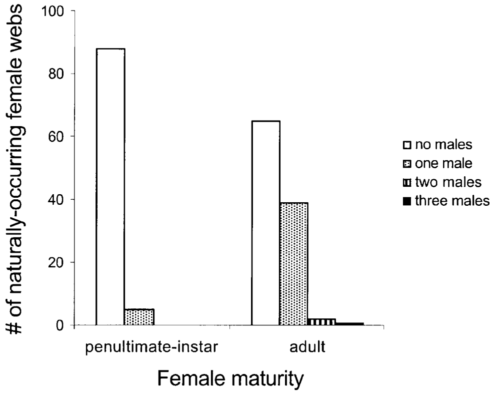


Figure 5.—Male residency in relation to female maturity in naturally-occurring webs. Number of males residing in each web (zero, one, two, or three males) is plotted against the number of naturally-occurring female webs with respect to female maturity. These data are the result of an early field survey.

30 times and each penultimate-instar female web site ($n$ = 27) was checked an average of 27 times. The proportion of observations that a female's web site was visited by a male and the number of different males involved was recorded for each female. Each female then served as a single observational unit for the purpose of analyses. All analyses used data from the entire study period, except for the duration of male-female encounters and mating analyses, which used data collected after the first day (when male marking began). Except where noted, only data concerning present and live spiders were analyzed.

Data from the two sets of animals (those placed into the field on 8 and 13 July) were combined when they exhibited no significant differences. Percentage data were arcsine square root transformed prior to analysis. Duration data, which were non-normally distributed, were analyzed using nonparametric tests. Summary statistics of continuous variables are reported as $\bar{X}$ ± standard error (SE). Alpha was set at 0.05 for all tests and all tests are two-tailed. Data were analyzed with the JMP IN (version 4.0.3; SAS Institute Inc. 2001) computer package, or, in the case of rates of male arrival, with Systat (Systat Software, Inc.).

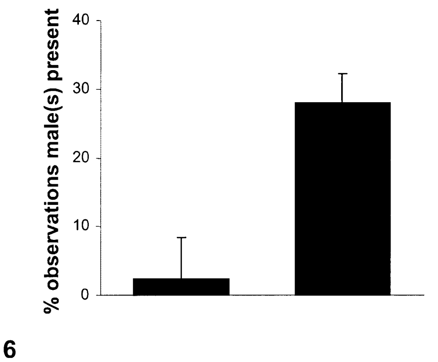
## RESULTS

**Male residency in relation to female maturity: naturally-occurring webs.**—Male cohabitation with immature females was rarely observed in naturally-occurring *A.* cf. *jucundus* webs during our early census. The webs of adult females were far more likely to contain an adult male (42 of 107 females, 39.3%) than were the webs of penultimate-instar females (5 of 93 females, 5.4%; $\chi^2 = 35.79$, $P < 0.0001$). Of those webs that contained males, most adult females ($n$ = 39) and all five penultimate-instar females each contained a single male. Two of the adult females each cohabited with two males, and the web of one adult female contained three male visitors (Fig. 5). Since we were interested in male residency with females and female-female residency was rare, four webs that each contained two adult females and two webs that each contained two penultimate-instar females were excluded from the previous analysis.

All penultimate-instar males were found as solitary individuals ($n$ = 48). In contrast, at least as many adult males were found with a female ($n$ = 46) as without ($n$ = 38). In one additional case, three adult males were found together in one web without a female.

**Male residency in relation to female maturity: artificially-established webs.**—Of the females placed into the field, many (47 of 81, 58.0%) disappeared from their web sites before the study ended. The web sites of adult females were, again, far more likely to contain an adult male than were the web sites of penultimate-instar females (27.9 ± 4.3% versus 2.4 ± 6.1% of the observations per female; $n$ = 36 and 18 females, respectively; $t_{52} = 3.41$, $P = 0.0013$; Fig. 6). Adult females also had a greater number of male cohabitants per hour (0.37 ± 0.06) than did penultimate-instar females (0.03 ± 0.08; $t_{52} = 3.28$, $P = 0.0019$; $n$ = 36 and 18 females, respectively; Fig. 7). All but five (of 54) male visitations were by new, unmarked males. The five exceptions included one male who returned to the same female after a 37 hour absence, two males who each traveled to a second female, and one male who traveled to three different females.

Although males appeared to arrive to adult female web sites at twice the rate than to subadult female web sites (to 33 out of 118 available adult females, or 28%, versus 6 out of 43 available subadult females, or 14%), this difference was not statistically significant with our sample size (Mantel-Haenzel $\chi^2 = 2.37$, $P = 0.12$, for the comparison of numbers of new



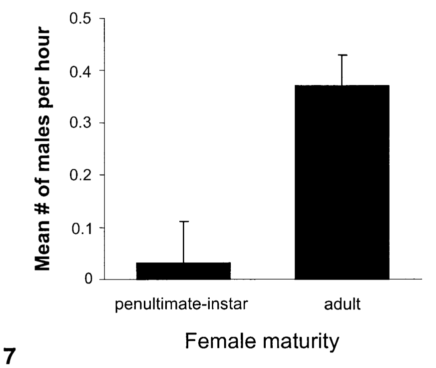


Figure 6.—Male residency in relation to female maturity in artificially-established webs: percent of field observations in which at least one male was present (± SE).

Figure 7.—Male residency in relation to female maturity in artificially-established webs: mean number of male residents per hour (± SE).

males arriving per total females available at each of 18 different census periods). Males also tended to stay longer at adult female web sites (see next section), but this effect appeared to reflect whether copulation occurred or not, rather than female age per se.

**Duration of male residency.**—Because of the periods between census days during which the nests were not monitored, we can only provide estimates of the minimum and maximum possible male residence times. In cases where male residence periods had either already been initiated when observations had started or had not yet concluded when observations ended, we have taken the period actually observed as the minimum male residence time. This period plus the unobserved period either before or after the start of a census day, as appropriate to the case, gives us a maximum possible residence time. Given these considerations, the median male residence time we observed was bracketed between a minimum of five and a maximum of 11 hours.

Based on our minimun male residence estimates (period actually observed), males spent more time per visit with adult females with whom they mated than with any other females (median = 18.5 hours, versus 5 hours for adults not observed to mate, and 3 hours for penultimate-instar females; $n$ = 10, 37, and 6 visits, respectively; $\chi^2$ = 12.1, 2 df, $P$ = 0.002; Fig. 8). Post-copulatory periods ranged from three to 33 hours ($n$ = 10), with seven cases lasting seven hours or less. If three cases in which the period had not yet concluded when observations ended are included, a floor for the median post-copulatory period is estimated at six hours.

In a few instances, more than one male could be observed at a female's web site (Table 1). Cohabiting males engaged in agonistic interactions, including foreleg tapping and locking of chelicerae and legs ($n$ = three pairs of males in the presence of three different females). One battle sent a male tumbling and appearing temporarily dead (Fig. 4), while his combatant copulated with the resident female (Fig. 3). Male–induced *coitus interruptus,* resulting in no resumption of copulation, was also observed in one case where two males were simultaneously present with a female.

**Mating frequency.**—Nineteen of the 36 adult females (52.7%) were observed mating with at least one male over the study period. Eleven of these females (57.9%) were each observed mating with a single male. The remaining eight of these females (42.1%) were each observed mating with two males. The average number of males a female copulated with over the active observation period (an average of 38.8 observation-hours per female) was therefore 0.75, which corresponds to 0.47 males per female per day, if we assume a similar mating rate during non-observed periods, or, more conservatively, 0.22 males per female per day if we assume that all matings were observed during the recorded period of each female.

Some marked males (10 of 76, 13.2%) were observed at the web sites of two ($n$ = 9) or

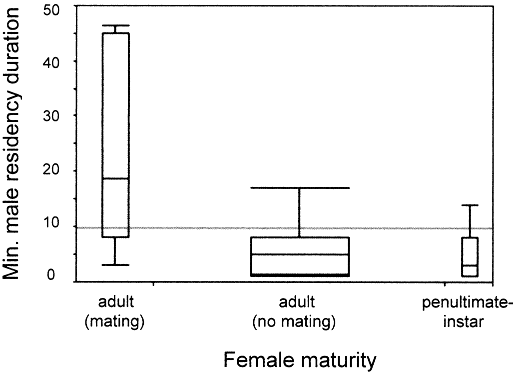


Figure 8.—Estimates of the range (outermost lines in each graph), 25th and 75th quantiles (edge of boxes), and medians (lines inside the boxes) of the minimum duration of male residency (based on period actually observed) with respect to female age and mating status. Males spent more time per visit with adult females with whom they mated (median = 18.5 hours; *n* = 10 visits), than with adults with whom they were not observed to mate (median = 5 hours; *n* = 37 visits), or with penultimate-instar females (median = 3 hours; *n* = 6 visits).

three (*n* = 1) females. However, because males could not be tracked as reliably as females (and several of the females were absent or dead at the time of male visitation), only one of these males was actually observed to mate more than once. Overall, ten of 48 (20.8%) visits by marked males to adult female web sites were observed to result in copulation (Fig. 8).

Measurements of distances between female web sites that males successively visited showed an average travel distance of 2.0 ± 0.4 m (range: $<$ 1–4 m, *n* = 11 males) over an average of 21.5 ± 4.5 hours (range: 11.5–51.0 hours, *n* = 11). Three of the males each traveled four meters in an average 32.3 ± 11.4 hours.

## DISCUSSION

*Anelosimus* cf. *jucundus* males were much more likely to be found on the webs of adult females than on those of penultimate-instar females, both in a survey of free-ranging spiders and when females of known age and reproductive history were placed into the field. Adult females also had a greater number of male residents per hour than did penultimate-instar females.

The mechanism responsible for these divergent residency patterns remains unclear. Males could preferentially arrive at the webs of adult females or arrive equally at both adult and juvenile female webs, but be preferentially retained by adult females. Our data show a nonsignificant trend towards differential arrival at adult webs and significant retention when copulation occurs. Although a greater sample size will be needed to definitely address this issue, the trend towards preferential arrival at adult female web sites suggests that females may be producing a distance-acting signal or cue guiding males to their webs. Distance-acting pheromones released by females have been demonstrated to attract males in both *Pardosa milvina* wolf spiders (Searcy et al. 1999) and in *Agelenopsis aperta* desert spiders (Papke et al. 2001). If males arrive at the webs of adult and juveniles equally, then some process associated with interaction with the female must influence duration of male residency.

Nearly half of the females observed mating copulated with more than one male, suggesting that multiple mating by females is common in this species. Matings were not predictably followed by continued male residence at the females' web sites (in 60% of the cases the male departed in six hours or less), so prolonged post-copulatory guarding appears to be absent in these spiders. Male residency subsequent to copulation could simply involve time spent by males inducting sperm into their pedipalps for subsequent matings or their facultative use of females' webs for food and shelter, rather than a means of exploiting the resident females' reproductive biology. Given that males differentially reside with adult females, females multiply mate, and males do not exhibit post-copulatory guarding, male mating order may not be an important determinant of paternity in *A.* cf. *jucundus*.

At times, more than one male entered the same adult female site. This could result in multiple matings by females with different resident males, or male-male aggressive interactions, as described earlier. Because of the scarcity of extended multiple male residencies, aggressive interactions may drive some males to search for different, unattended females.

Many adult females were observed mating during the relatively short study period. Of

Table 1.—Number and proportion of census observations with zero, one, two, or three males cohabiting with adult females in their artificially-established webs. Multiple male residency at a given female's web was uncommon. Calculations are pooled across females.

| # males | # observations | % observations |
|---|---|---|
| 0 | 355 | 57.1 |
| 1 | 211 | 33.9 |
| 2 | 53 | 8.5 |
| 3 | 3 | 0.5 |
| Total | 622 | 100 |

those females, about half were observed to mate with at least two males. Given that females become sexually receptive an average of ten days after the final molt and cease sexual receptivity after oviposition (Bukowski & Avilés 2002), a total of 20 days spans the average period of sexual receptivity for females in this species. Assuming that a female's propensity to mate does not alter dramatically over the course of these 20 days and that all matings are considered to have been observed throughout the period of censusing, a female may be calculated to mate with an average of 4.4 males during her lifetime (0.22 males per female per day × 20 days). This figure may underestimate the number of potential matings if we assume that additional matings occurred during the unobserved periods. Alternatively, this figure may overestimate the number of potential matings if female receptivity or the frequency of male visitation to females' web sites diminished as the 20-day female active period progressed, although we have no evidence negating or supporting either a diminished female receptivity or reduced male visitation over time. All matings within census days were likely to have been observed and recorded because times between censuses were shorter than the average copulation duration. Matings occurring during the much longer period between census days, on the other hand, could have been missed.

The male residency and female mating patterns exhibited by *A.* cf. *jucundus* have important implications for the pattern of sperm utilization at fertilization. When the fertilization pattern is biased towards first males, males differentially cohabit with juvenile females approaching the final molt when the females first become sexually receptive (Austad 1982; Christenson & Cohn 1988; Watson 1990; Bukowski & Christenson 1997; Bukowski et al. 2001). When the fertilization pattern is biased towards last males, males should preferentially seek out and guard adult females (Uhl 1998; West & Toft 1999). When the sperm of two or more males mix equally within the female, males should seek out adult females regardless of female age (Eberhard et al. 1993). Our data suggest that *A.* cf. *jucundus* exhibit either last male precedence or sperm mixing. Other data on sperm release patterns in this species, along with no evidence of mate guarding, provide support for sperm mixing, since the first and second males to mate with a female were found to transfer equal numbers of sperm (Bukowski & Avilés, unpub. data). Several studies have shown that when two males mating with a female transfer equal numbers of sperm, the two males typically sire equal numbers of offspring (Bukowski & Christenson 1997; Schneider et al. 2000; Elgar et al. 2000). If a male were to reside with a penultimate instar female until she became sexually receptive, he would likely visit and mate with fewer females, siring fewer offspring than a male that exclusively visits adult females.

Understanding the role of female maturity, mating receptivity and subsequent sperm utilization is contingent upon learning more about the natural history of *A.* cf. *jucundus* spiders. Precisely determining male arrival rates and residency durations relative to female maturity could serve as the next step in understanding the mechanisms driving their sexual interactions.

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