Mating patterns in late-maturing female Mediterranean tarantulas may reflect the costs and benefits of sexual cannibalism

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During courtship and mating, males of some invertebrate predators risk being killed and consumed by females, who in turn can obtain a foraging benefit from feeding on males. In these invertebrates, the sex ratio at the end of the mating season is usually female biased, probably due to sexual cannibalism and other sources of male mortality. Thus, at the end of the mating season males can be a limited resource to females as both mates and prey. Because of the high risk incurred when approaching females, males should show mate choice. To date there are little data on the costs and benefits of sexual cannibalism in natural populations. For one month we followed the mating patterns of 60 late-maturing Mediterranean tarantula, *Lycosa tarentula* L., females in a desert grassland population. The later a female matured, the shorter was her cohabitation time with males and the lower her probability of cohabiting with a male at all, suggesting that late-maturing females may be limited in their access to males as mates. At the end of the mating season, nonsexually cannibalistic late-maturing females also had poorer body conditions than did both sexually cannibalistic late-maturing females and early-maturing females, suggesting that late-maturing females may be also limited in their access to males as food. Females had higher mating success if they were smaller or in better condition (better fed). This pattern may reflect either male choice, or the possibility that small, well-fed females have higher mating success because they are less aggressive towards males.

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Sexual conflict can be quite extreme in those invertebrate predators in which males can become the prey of their potential partners (Elgar 1992; Schneider & Lubin 1998). In these species, males should approach females cautiously to avoid becoming prey. On the other hand, females may benefit from feeding on males (e.g. Johnson 2001), especially if prey availability is low. However, by killing males before mating, females risk remaining unmated (Elgar 1992), particularly when males are scarce. In these invertebrate predators, the sex ratio is female biased at the end of the mating season, probably due to sexual cannibalism and other sources of predation (Christenson & Goist 1979; Austad 1982; Hurd et al. 1994). Therefore, at the end of the mating season, males can be a potentially limiting resource to females. When males have few mating opportunities and are of value to females as a meal, males could contribute to the female

reproductive output and thus should be more willing to offer themselves as prey to their partners after copulation (the paternal investment hypothesis: Thornhill 1976; Parker 1979; Buskirk et al. 1984). A prediction of the paternal investment hypothesis is that males that behave in a manner that favours postcopulatory cannibalism should prefer to mate with larger, more fecund females (Thornhill 1976). Higher fecundity in arthropod females is correlated with a larger fixed size (i.e. carapace or pronotum width) and a better body condition (i.e. abdomen width controlled for fixed size, which is a measure of stored reserves). However, because there is a cannibalistic risk involved in approaching a female, a male may prefer to mate with a female with a larger carapace width or in better body condition because she is likely to lay more eggs, independently of whether he offers himself as a meal (the fecundity advantage hypothesis: Jones et al. 2002). Alternatively, he may prefer to mate with a female in better body condition because her hunger state is low and therefore she is less likely to attack him (the cannibalism avoidance hypothesis: Lawrence

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1992). Within sexually cannibalistic invertebrates, there are two documented cases in mantids (Lawrence 1992; Maxwell 1998) and one in spiders (Prenter et al. 1994) in which males prefer heavier females. In contrast, Riechert & Singer (1995) did not identify male choice for larger females in the funnel-web spider *Agenelopsis aperta*. Evidence suggests that less hungry females are less likely to attack males in mantids (Liske & Davis 1987; Birkhead et al. 1988; Kynaston et al. 1994) and in one spider species (Andrade 1998).

The Mediterranean tarantula, *Lycosa tarentula* (L.), is a territorial, cannibalistic burrowing wolf spider (Fernández-Montraveta & Ortega 1990a; Moya-Laraño et al. 1996, 2002). During the mating season, we followed late-maturing females for one month, documenting their mating patterns, the frequency of sexual cannibalism, the potential benefit that females obtained from sexual cannibalism, the degree to which males might be a limited resource and the potential for male choice.

MATERIAL AND METHODS

The Study Species and Study Site

The Mediterranean tarantula lives in open areas across the Mediterranean region (Fabre 1913; Ortega Escobar 1986; Orta et al. 1993). Females remain inside the burrow during daylight and forage outside the burrow during the night (Ortega et al. 1992). The study was conducted in the desert grassland of Cabo de Gata (Almería, Spain). *Lycosa tarentula* females are food-limited (Moya-Laraño et al. 1998; Moya-Laraño 2002). Details about the study site are described elsewhere (Moya-Laraño et al. 1998, 2002). In this population, males account for up to 30% of the biomass intake by females and are one order of magnitude more profitable than the most common prey (Moya-Laraño et al. 2002).

Data Collection

All data were recorded within the mating season of *L. tarentula*, from 1 to 30 June 1997. During 1–4 June we marked, measured and released all encountered sub-adult females back into their burrows (techniques are described in Moya-Laraño et al. 1996; Moya-Laraño 1999). Spiderlings hatch in September–October and reach maturity in May–July during the second season, almost 2 years later. Mature males disappear completely from the population during July–August (Fernández-Montraveta et al. 1991; Orta et al. 1993; Moya-Laraño et al. 1996; Parellada 1998). Because of this highly seasonal pattern, antepenultimate instars were not present at the time of our observations. A reflecting flag was planted beside each burrow to facilitate location. Each spider was immobilized in fine mesh and its carapace and abdomen widths were measured with a caliper (± 0.1 mm) so that we could use the relationship between carapace width and abdomen width as a measure of body condition. Spider body condition, which is an indirect measure of energy and nutritional reserves stored in the abdomen,

can be measured in different ways (Jakob et al. 1996; but see Kotiaho 1999; Marshall et al. 1999). In *L. tarentula*, abdomen width, with the correlation with carapace width removed, is a good indirect measurement of female reproductive success, because a higher body condition before laying an egg sac is correlated with a higher probability of survival, a shorter time to egg laying and a larger egg sac, which tends to produce more and heavier offspring (Moya-Laraño 2002).

Females can potentially make a second egg sac, but data from other populations show that females produce a second egg sac only if they survive for a second season (Fernández-Montraveta & Ortega 1990b; Parellada 1998; Moya-Laraño 2002). Censuses in early spring showed no adult females in the population (J. Moya-Laraño, personal observations). This finding, and the fact that second-year reproductive females are easily distinguished from first-year reproductive females because of the lack of hair in the former (Moya-Laraño 2002), indicates that in the study population there were no second-year reproductive females.

Before being released back into their burrows, we marked each spider on the legs with enamel paint using a code for individual identification. After maturing, each female was measured and marked again. We could be certain that a female had moulted because we usually found the exuviae inside or beside the burrow, and because the spider showed a pale coloration that was correlated with a decrease in body condition and an increase in fixed size. If we found no evidence of moulting, and if the spider had no mark, a dark coloration and a good body condition, all indications that the spider moulted a long time ago, we concluded that the burrow had been invaded by another spider, which probably came from a part of the population that was not being monitored. We searched for remains of the original owner, which would indicate that the invading spider had cannibalized the previous owner. Each newly encountered male was captured, marked and released in the same place in which it was found. We visited each female consecutively from 1000 to 1600 hours at least once every day, and once every 2 days at night, between 2200 and 0300 hours. In each visit, we searched for males cohabiting with females and recorded mating events. Males either abandoned the female within the next 12–24 h or stayed with her for up to 6 days. Because we could not know the exact time when a male either arrived or abandoned each female, we considered that a male that was cohabiting with a female on one occasion had been cohabiting with her for 24 h. A male that was observed on one occasion and again 24 h later with the same female was considered to have been with the female for 2 days, and so on. Although likely an overestimation of the actual time that a male spent with a female, this convention provided a relative measure of the time that each female spent with a male, allowing the distinction between females that had never been observed with a male (0 days) from the females that had been observed once with a male (1 day). Because mating lasts for about 90 min (Fernández-Montraveta & Ortega 1990b), mating couples were visited again after 2 h to determine whether

the encounter had ended in sexual cannibalism (i.e. the male had been consumed by the female inside the burrow), or if the male had left. The presence or absence of the female and the causes of disappearance, when known, were recorded. Foxes dig spider burrows and presumably feed on them (Moya-Laraño 2002; Moya-Laraño et al. 2002). Burrows dug by foxes are easily recognized. Because all spiders were initially measured and marked in a 4-day period, day 4 (4 June) of the experiment was set equal to time zero for all spiders, which guaranteed that timing measurements were homogeneous for all of them.

At the end of the study, we compared the body condition of late-maturing females with that of a simultaneous sample of females from this population that was the focus of another study (Moya-Laraño et al. 2002). Most of these latter spiders, which were captured again in the simultaneous study mentioned above, were captured and released at the beginning of the present study but had not been marked because they were already mature; therefore, we could be certain that most of these spiders were early-maturing females. By comparing the spiders that we had collected as subadults and that had matured by the end of the study (late-maturing females) with a sample of females from the rest of the population (early-maturing females), we could assess the effects of late maturation on body condition. In the same analysis, we compared the body condition of three female groups: (1) late-maturing sexually cannibalistic females (i.e. females that were observed feeding on a male), (2) late-maturing non-sexually cannibalistic females (i.e. females that were not observed feeding on a male) and (3) early-maturing females of unknown cannibalistic and mating history. We predicted that late-maturing sexually cannibalistic females would have benefited from sexual cannibalism and thus would have better body conditions after cannibalism than would late-maturing nonsexually cannibalistic females. Furthermore, if each early-maturing female had had access to at least one male as food, then the body conditions of late-maturing sexually cannibalistic females and early-maturing females would not differ significantly, indicating that early-maturing females had the same access to food as sexually cannibalistic late-maturing females. However, we predicted that the body conditions of nonsexually cannibalistic late-maturing females would be significantly smaller than those of early-maturing females, indicating that late-maturing females were limited in their access to either males as food or to other sources of food. Although we could have missed some sexually cannibalistic events because of our sampling schedule, and therefore erroneously assigned some females to the nonsexually cannibalistic group, males are 10 times more profitable than the most common prey (Moya-Laraño et al. 2002), which should make the effect of the observed sexual cannibalism on female body condition detectable even with the introduction of some bias.

Estimation of Female Mating Success

We estimated female mating success in two ways: number of matings per female, and cohabitation
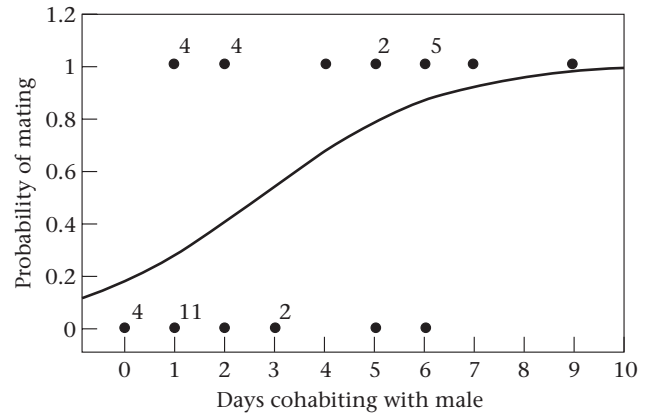

Figure 1. The longer a female cohabited with any male, the higher was the probability that she was observed mating. Therefore, cohabitation length is a good predictor of female mating success. The number beside each dot indicates number of overlapping data points.

duration, which is correlated significantly with the probability of mating. The total number of days that a female was observed cohabiting with any male predicted whether she was observed mating at least once (logistic regression: $\chi^2_1 = 11.7$, $P < 0.001$; Fig. 1). Each additional day cohabiting with a male increased the probability of mating for a female by 0.14 (see Allison 1999 for calculation of effects). Therefore, females that were observed more than 6 days with a male had a 100% chance of being observed mating. Six females were observed mating twice, and the total number of cohabiting days also predicted the total number of mating events observed for each female (Spearman rank correlation: $r_S = 0.640$, $N = 38$, $P < 0.001$). This pattern indicates that mating without previous cohabitation is much less likely than mating after a long cohabitation period. Because the duration of cohabitation showed higher variation than the number of observed mating events (i.e. 0–9 days for cohabitation duration versus 0–2 observed matings per female), duration of cohabitation can be analysed with higher statistical power. Furthermore, in our scheduled visits, we probably missed some mating events. For these reasons, we analysed cohabitation as a measurement of mating success in addition to analysing the number of observed matings per female.

Statistical Analyses

When body condition was used as an independent variable in a multiple regression analysis, we included abdomen width and carapace width in the model. Because abdomen width is statistically controlled for by carapace width (i.e. fixed size), in such an analysis abdomen width measures body condition independently of spider size (Moya-Laraño 2002). On the other hand, when body condition was the dependent variable (i.e. when we compared body condition between groups), we used the ratio between abdomen width and carapace width as an index of body condition (Jakob et al. 1996). Regression residuals were not used because their use is

potentially misleading (Kotiaho 1999; García-Berthou 2001). The effects of maturation time and sexual cannibalism on body condition were tested with Kruskal–Wallis analysis of variance (ANOVA). The differences between groups were compared by post hoc comparisons (Siegel & Castellan 1988) followed by the sequential Bonferroni procedure (Rice 1989). Because we predicted the directions of all effects in our comparisons (see the above section), post hoc comparisons were all one tailed. Using the ratio as body condition may be also misleading, and therefore the recommendation of using analysis of covariance (ANCOVA; García-Berthou 2001) was also followed because, in spite of the very small sample size, the assumptions of homogeneity of variances and homogeneity of slopes were met, and the lack of an appropriate normality test was overcome by running a multiple regression randomization test, which is not restricted by the normality assumption for linear models (Anderson & Legendre 1999). We included the three groups to be compared in two dummy variables (Zar 1996). The ANCOVA assumption of homogeneity of slopes was corroborated by testing the interaction between carapace width and the dummy variables.

The influence of different variables on a given dichotomous response variable was measured using logistic regression (Allison 1999; see Hardy & Field 1998 for a comprehensive example of its use in animal behaviour). We tested for interactions by comparing the log-likelihood value of logistic regression models with and without interactions. Interaction terms were calculated as the product of the involved variables. To minimize multicolinearity, before calculating the interaction term, each variable was centred to zero by subtracting the variable mean from each value (Jaccard et al. 1990).

The logit ordinal multinomial model was used to regress the number of matings per female (one measurement of mating success) on spider size, body condition and day of moulting (Allison 1999). Again, the interaction terms and significance tests were calculated following Jaccard et al. (1990).

Because some spiders were still alive but had not received a male by the end of the study, we tested the influence of time to moult on the time to receive the first male using parametric survival regression analysis (SRA), which accommodates censored data (Allison 1995; see Moya-Laraño & Wise 2000 for a comprehensive example about its use in animal behaviour). We used SAS to calculate SRA models (Allison 1995).

To test whether two proportions differed from an expected 1:1 ratio, we used the log-likelihood ratio test (G) with the Williams correction for continuity (Sokal & Rohlf 1995). If the expected values differed from 1:1, we used the binomial test (Siegel & Castellan 1988).

RESULTS

Mortality Pattern

We extracted 242 females from their burrows, 180 (75%) of which already were adults and were not included in the study. Therefore, the 60 subadult females
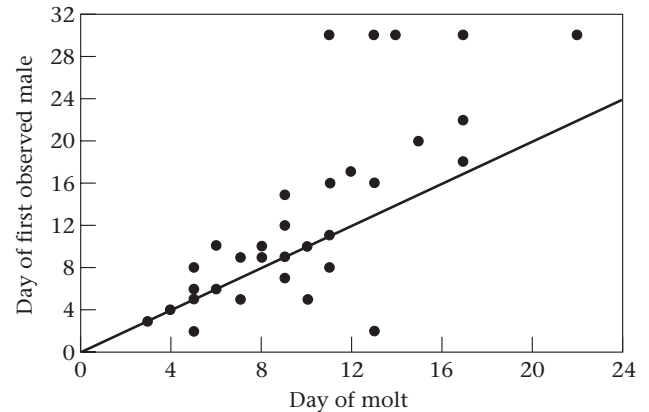

Figure 2. Positive relationship between female maturation time and male arrival time. The line indicates the 1:1 expected slope if males reach females at exactly the time when the latter mature. Points above the line indicate females that received a male after maturation, and points below the line are those females that received a male before maturation. The male that visited a female long before she moulted (outlier at the bottom), abandoned her immediately (i.e. he was not found in the next visit), but the other five males that reached an immature female cohabited with her until she matured. On average, the first male was observed with a female a few hours after she moulted. The five upper points are those females that never received a male (censored data; see text for statistical analysis).

included in our study were late-maturing females. Of the 60 marked penultimate females, 38 survived to maturity, but only 13 mature spiders were still in their burrows at the end of the study (30 June), yielding a mortality rate for late-maturing females higher than 75%. Of the 47 females that disappeared, three were cannibalized by invading adult females; 13 were missing or were found far away from their burrow because a scorpion (*Buthus occitanus*) had invaded the burrow; two were attacked by red foxes, *Vulpes vulpes*; and two were killed by a spider-hunting wasp (*Cryptocheilus* sp.) (Pompilidae). The remaining missing spiders (N=27) disappeared from unknown causes.

Mating Patterns

Only the 38 females that reached maturity were considered for analysis. Each of these females was visited by an average of 1.3 ± 0.1 males (range 0–4) and was observed mating 0.6 ± 0.1 times (range 0–2). Whenever a female mated more than once, it was always with a different male. The date that a female was first observed cohabiting with a male depended on the date of female maturation (survival regression: log-logistic model: $\beta=0.135$, SE=0.018, generalized $R^2=0.618$, $\chi^2_1=36.15$, N=38, $P<0.001$; Fig. 2). After translating the beta coefficient into the effect of time to moult on time to first male by using the expression $100(e^\beta - 1)$ (Moya-Laraño & Wise 2000), we concluded that an increase of one unit of time to moult (i.e. 1 day) increased the time to receive the first male by about 14%. This relationship led to the conclusion that the first male was observed cohabiting with a female approximately 3 h after she had moulted.

Table 1. Results of a multiple regression analysis of the influence of carapace width (fixed size) and abdomen width (body condition), controlled for day of moulting, on the number of days that a female was found cohabiting with males

Variable	Slope	SE	t_{34}	P
Carapace width	−1.69	0.56	−3.03	0.005
Abdomen width	1.69	0.46	3.65	<0.001
Day of moulting	−0.27	0.08	−3.55	0.001

Table 2. Results of a multiple logistic regression analysis (ordinal multinomial logit model) of the influence of carapace width (fixed size), abdomen width (body condition) and day of moulting, on the number of matings per female (0, 1 or 2)

Variable	Slope	SE	χ_1^2	P
Carapace width	−1.64	0.73	5.09	0.024
Abdomen width	1.69	0.59	4.29	0.038
Day of moulting	−0.15	0.08	3.53	0.060

Table 3. Results of a multiple logistic regression analysis of the influence of carapace width (fixed size), abdomen width (body condition) and day of moulting on the probability of male limitation (i.e. probability of a female not receiving a male after moulting)

Variable	Slope	SE	t_{34}	P
Carapace width	0.99	0.99	1.00	0.324
Abdomen width	−0.37	0.58	−0.63	0.533
Day of moulting	0.31	0.13	2.35	0.025

Although we probably missed some mating events, visiting females more often during the daytime than at night allowed us to minimize the number of mating events missed, because mating is unlikely to occur during night hours. Of the 21 females that we observed mating, only 15 had been observed cohabiting with males both during the day and at night. Therefore, these 15 females were the only ones that, according to our scheduled observations, had the chance of mating in either period. Thus, for testing whether mating was more likely during the day or during the night, we included only those 15 females that were observed with males in both periods. The remaining six females were observed either only once with a male or more than once but always in the same period (day or night). This is a conservative test, because it removes the possible effect of day–night differences in cohabitation. Because we visited the population more often during the day ($N=28$) than during the night ($N=16$), we adjusted the expected probabilities for differences in sampling effort: $p(night)=16/44$ and $q(day)=28/44$. Mating was significantly more likely to occur during the day ($N=15$ mating events) than during the night ($N=0$ mating events) (binomial test: $P=0.004$).

Female Mating Success

Females showed higher mating success if they moulted earlier, were smaller and had better body conditions. We included in a multiple regression analysis carapace width, body condition and day of moulting as independent variables and the time cohabiting with males (i.e. one estimate of mating success) as the dependent variable. The later a female moulted, the shorter the period that she cohabited with males (Table 1). The larger the female (correcting for time of moulting), the less time males cohabited with her, and the better the female body condition, the longer males cohabited with her. Neither a model including two-way interactions (difference between coefficients of determination: $F_{3,31}=0.01$, $P=0.999$) nor the model including the three-way interaction was significantly different from the model without interactions (difference between coefficients of determination: $F_{4,30}=0.00$, $P=1.000$). When we used the total number of matings per female as a measurement of mating success, the output of the logit model was very similar, although the P values were one order of magnitude lower (Table 2). The model without interaction terms was significant ($\chi_3^2=8.88$; $P=0.0310$) but neither a model including two-way interactions, nor one including

the three-way interaction, was significantly different from the model without interactions ($\chi_3^2=3.26$, $P=0.473$ and $\chi_4^2=2.81$, $P=0.531$, respectively).

Male Limitation

One-fifth of the 38 mature females were never observed with a male after they became adults. A multiple logistic regression analysis predicting the probability that a female was not found with a male was significant based upon the day of moulting (logistic regression: $\chi_3^2=8.26$, $P=0.041$; Table 3), but neither the carapace width nor the body condition predicted this probability. Neither a model including two-way interactions ($\chi_3^2=3.26$, $P=0.353$) nor a model including the three-way interaction was significantly different from the model without interactions ($\chi_4^2=2.81$, $P=0.590$). Every additional day of delay in moulting increased the probability by 4% that a female would not be seen with a male.

Sexual Cannibalism and Differences between Early- and Late-maturing Females

We observed two adult females feeding on a male. One female had received three other males (the only spider in the population that received so many males) and the other received no additional males. We were unable to determine whether the two cannibalistic instances occurred after mating or whether the female killed the approaching male without mating with him. None of the observed mating events ($N=24$) ended in cannibalism.

Thirteen out of 38 females that had matured survived from maturation to the end of the study. Of those 38 females, the ones that had consumed a male tended to have a higher chance of surviving to the end of the study (2/2) than did those females that were not observed consuming a male (11/36) (G test with Williams correction: $G_1=4.51$, $P=0.062$).
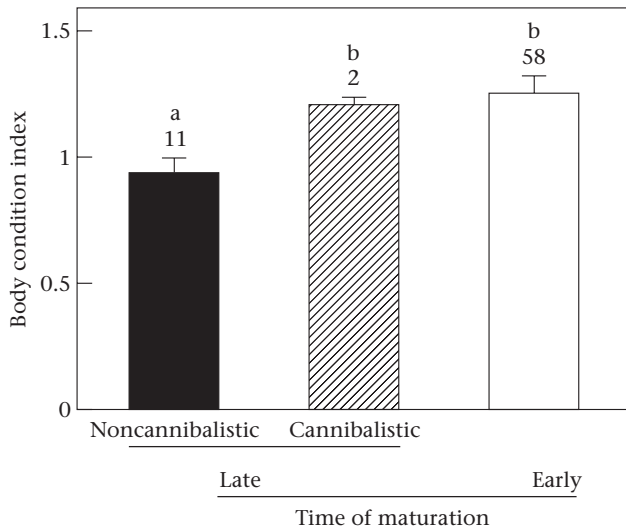
Figure 3. At the end of the study, cannibalistic females (those observed feeding on a male) had a higher body condition index (abdomen width/carapace width) than noncannibalistic females, but cannibalistic females had the same body condition as early-maturing females of unknown cannibalistic history. Numbers above bars indicate sample sizes. Groups with different letters ('a' or 'b') were significantly different from each other (statistical analyses are shown in the text).

Both early-maturing females and sexually cannibalistic late-maturing females had better body conditions than late-maturing nonsexually cannibalistic females. Both a Kruskal–Wallis test and a randomization test comparing the body conditions of late-maturing sexually cannibalistic females, late-maturing nonsexually cannibalistic females and early-maturing females of unknown sexually cannibalistic history were significant (Kruskal–Wallis test: $H_2 = 13.41$, $P = 0.001$; randomization test: $P = 0.002$; Fig. 3). Late-maturing sexually cannibalistic females had significantly better body conditions than did late-maturing nonsexually cannibalistic females (Kruskal–Wallis post hoc comparison: $P = 0.014$; randomization test: $P = 0.018$). Early-maturing females and sexually cannibalistic late-maturing females had similar body conditions (Kruskal–Wallis post hoc comparison: $P = 0.330$; randomization test: $P = 0.482$), whereas early-maturing females had better body conditions than did late-maturing nonsexually cannibalistic females (Kruskal–Wallis post hoc comparison: $P < 0.0001$; randomization test: $P = 0.0001$).

DISCUSSION

Female Benefit from Sexual Cannibalism

Our preliminary results show that sexual cannibalism may benefit adult *L. tarentula* females. Females found feeding on a male tended to have a higher probability of survival and better body condition than did spiders that were not observed feeding on a male. Because we could have missed some cannibalistic events occurring in the animals assigned to the nonsexually cannibalistic group, our test is conservative. Although we did not measure fecundity in the present study, another *L. tarentula* study

documented that body condition is positively correlated to several female fitness parameters (Moya-Laraño 2002). In addition, other research on *L. tarentula* suggests that males may be a major source of food for females (Moya-Laraño et al. 2002), contributing to the alleviation of female food limitation. Although we cannot draw strong conclusions because of our small sample size, the observations reported here provide tentative evidence that female *L. tarentula* can obtain a significant benefit from feeding on males.

Evidence against the Paternal Investment Hypothesis

The observed pattern was not consistent with the prediction of the paternal investment hypothesis (i.e. that males should offer themselves as prey to the females with whom they have mated; Thornhill 1976; Parker 1979; Buskirk et al. 1984). In all observed matings, males left females without being cannibalized. Although we probably missed some mating events, we were certain than none of the 24 observed copulations finished in cannibalism. The paternal investment hypothesis predicts that male sacrifice after mating if (1) the male is a significant source of food to the female and (2) chances of mating more than once for the male are very small. Although the first assumption is met by *L. tarentula*, the second assumption is not, because females are willing to mate more than once, therefore providing the males with extra chances for remating if they do not sacrifice themselves. In fact, paternal investment from sexual cannibalism is not predicted for wolf spiders (Buskirk et al. 1984). Males did not offer themselves as prey at the end of the season when mating opportunities were at a minimum and they would obtain the maximum benefit by doing so, which suggests that males do not ever offer themselves as prey to females, and that the paternal investment hypothesis of sexual cannibalism does not apply to *L. tarentula*. Future research will have to test whether, by escaping from female attacks, male *L. tarentula* increase their reproductive success by mating with other females. Males can also increase their reproductive success by being choosy (i.e. by preferring to mate with the less dangerous females in the population).

Female Mating Success: Male Choice or Female Aggression?

The pattern of male–female cohabitation and mating suggests either that males choose the less dangerous (i.e. small, well fed) females in the population or that these females are less aggressive towards males. The cohabitation and mating patterns suggest that males appeared to prefer small females and also females in good condition (i.e. low hunger state), supporting the cannibalism avoidance hypothesis. Male choice for small females is a surprising result. If males were picky, one would expect males to prefer large rather than small females, because larger female spiders have a higher expected fecundity (i.e. total number of eggs per clutch; e.g. Wise & Wagner

1992). However, in *L. tarentula* this trait may be relaxed because no positive correlation between female fixed size and fecundity has been observed (Moya-Laraño 2002). By selecting small females, males may decrease the risk of cannibalism, either by avoiding the most voracious females in the population or by decreasing their relative size to females, which may either increase the chances for males to escape cannibalistic attacks (Arnqvist & Henriksson 1997) or allow males to mate coercively with relatively smaller females (Clutton-Brock & Parker 1995). However, coercive mating should not be prevalent in a system in which males are a limiting resource because virgin females should be willing to mate with the scarce males. In sexually cannibalistic species, females in good condition are usually less likely to cannibalize males (Liske & Davis 1987; Birkhead et al. 1988; Kynaston et al. 1994; Andrade 1998). Thus, by choosing females in better condition, males may decrease the probability of cannibalism, thereby increasing their chances of mating with other females (Lawrence 1992). There is indirect evidence that *L. tarentula* females in better condition are less likely to cannibalize males (Moya-Laraño et al. 2003): females that had been artificially supplemented with food were more likely to be observed with a male after food supplementation, and control (nonsupplemented females), which were less likely to be observed with a male, increased their weight, as they would if they had eaten exactly one male. Differences in foraging effort between food-supplemented and control females could not explain these differences, supporting the hypothesis that control (i.e. hungry) females fed on a single large item (i.e. a male). The results of the present study also support the fecundity-advantage hypothesis because females in better condition show higher survival, have larger offspring and tend to be more fecund (Moya-Laraño 2002). However, because females may be more aggressive if they are relatively larger than the male and/or they are in poor condition, cohabitation and mating may be determined as much from female aggression as from male choice. Therefore, our results show that small females in good condition enjoy higher mating success, which may be the consequence of either male choice or female aggression. Further research is required to determine whether one or both hypotheses apply to *L. tarentula*, as well as to determine the potential effect of male size on female mating success.

Potential Cost of Late Maturation

Late maturation seems to be costly to *L. tarentula* females. First, 75% of late-maturing females disappeared from their burrows before reproducing, in three instances because early-maturing females invaded their burrows. This rate of 2.5% of the females disappearing per day is considerably higher than that observed in two other studies (0.3–1.3% disappearing per day during the breeding season; Moya-Laraño 2002; Moya-Laraño et al. 2002). Furthermore, the later a female moults, the higher is the probability that no male will reach her; in addition, the later a female matures, the shorter is the time that she cohabits with males, which is correlated with lower mating success. This lower mating success is probably not an artefact of our timing of observations, because after day 22 the number of cohabitation events in the population dropped to zero (Fig. 2), and none of the female spiders that were observed for an additional week were observed cohabiting nor mating with any male. Finally, late-maturing females may have a low access to males as prey. Early-maturing females had significantly better body conditions than did nonsexually cannibalistic late-maturing females, but had the same body conditions as those late-maturing females that were observed feeding on a male. Although rates of sexual cannibalism of early-maturing females were not recorded, the pattern suggests that late-maturing females may be limited in their access to males as food.

In conclusion, males seem to be a limiting resource for late-maturing females, and this limitation can be explained in terms of both males as mates and males as prey. This male limitation could have triggered the lower mating success of the most aggressive females, either because they were too intolerant of males or because males actively chose the less dangerous females.

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