Conflict or cooperation in the courtship display of the white widow spider, *Latrodectus pallidus*

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Abstract.   We used experimental manipulations to test adaptive explanations for the courtship display of the male widow spider, *Latrodectus pallidus* O. Pickard-Cambridge 1872. Two hypotheses have been suggested to explain a long and complex male display: a) Cooperation of males and females in the effort to physically stimulate the female. As the time of male arrival is not predictable, females may delay sexual readiness until the appearance of a courting male. b) Conflict between males and females regarding the display cost. Females impose on the males an energetically costly display that may last several hours as a test of their quality. To test both hypotheses, we manipulated the previous experience of either the male or the female. We presented naive or experienced males (males that had courted and were accepted by females but were prevented from copulating) to females that were either naive or experienced (had been courted by a male but prevented from copulating). We also presented naive males to mated females. Following the stimulation hypothesis, courted females were presumed to have been stimulated to mate and thus were expected to accept non-courting males as mates. Both naive and mated females, however, were expected to await male stimulation before allowing copulation. In contrast, the conflict of interest hypothesis predicts that the female tests each male for quality indicators and therefore a non-courting male should not be accepted as a mate. Mated females, however, should apply a less stringent test to courting males. Our results show that 1) naive females prevented males that did not perform a full courtship display from entering the nest and mounting; 2) naive males courted virgin females with the full display, independent of the female previous courting history; and 3) naive males shortened their courtship when presented with mated females. The results are consistent with the conflict of interest hypothesis.

Keywords: Sexual stimulation, male quality, sexual conflict, Theridiidae

Elaborate, conspicuous and time-consuming precopulatory displays are known in many animal taxa, including insects (Thornhill 1976; Svensson et al. 1990), fishes (Milinski & Bakker 1990), birds (Borgia 1995), and mammals (Behr & von Helversen 2004), with several hypotheses suggested for their function. These hypotheses, which are not necessarily mutually exclusive, postulate either a mutual interest of both male and female in courtship or a conflict between the two. Mutual interest may occur if the courtship enhances reproductive isolation (Mayr 1963; Dobzhansky 1970) by providing cues for species recognition (Ryan 1985; Andersson 1994) or if a long courtship is necessary to stimulate the female into mate (see reviews in Platnick 1971; Robinson 1982). A conflict may arise between males wanting to increase their fitness by mating as often and with as many females as possible, and females who increase their fitness by choosing the best male available (Trivers 1972; Parker 1979; Eberhard 1996). Conflict occurs when females choose males based on their courtship display, and subsequent escalation of the display imposes an increasing cost on the males, which reduces the males' fitness and the potential to mate with additional females (Andersson 1994; Eberhard 1996). Nevertheless, the male and female usually share an interest in mating, particularly when the chance of encountering mates is small (Segoli et al. 2006).

Some species of spiders have elaborate and costly precopulatory displays, including cutting the female's web, vibrating on the female lines, and drumming vigorously on the substrate (e.g., Robinson & Robinson 1980; Suter & Renkes 1984; Forster 1995; Parri et al. 1997). Understanding the role of males and females in shaping the courtship display in spiders is challenging in light of the cannibalistic behavior of females in many of these species (Elgar & Schneider 2004), since cues allowing for species recognition to avoid predation may be similar to those of mate assessment (Robinson & Robinson 1980; Andrade 1996; Schneider & Lubin 1998; Herberstein et al. 2002).

In order to test these two general explanations for the male courtship display, we investigated the courtship behavior of the white widow spider, *Latrodectus pallidus* O. Pickard-Cambridge 1872 (Theridiidae), inhabiting the Negev Desert, Israel, which belongs to a genus known for its sexually cannibalistic behavior (Ross & Smith 1979; Breene & Sweet 1985; Forster 1995; Andrade 1996; Segoli et al. 2006). Females of *L. pallidus* are large, sedentary predators, while adult males are less than a third of the female's size and, as in other *Latrodectus* species, actively search for females (Segoli et al. 2006). The female's web consists of a nest located in a shrub and connected by strong threads to a capture web consisting of a loosely woven platform and thin, prey-capture threads stretching from the platform to the ground (Lubin et al. 1991). In a similar species found in the same habitat, *L. revivensis* Shulov 1948, the male is attracted to the female's web by means of a female sex pheromone associated with the web silk (Anava & Lubin 1993). On the web, males engage in a vibratory display while cutting and removing sections of the capture web before approaching the female's nest and engaging in tactile courtship (Segoli et al. 2006, 2008). The courtship behavior has been described in several species of

Latrodectus (Kaston 1970; Ross & Smith 1979; Lubin & Anava 1993; Forster 1995), but not in *L. pallidus*.

To determine what factors shape the courtship display in *L. pallidus*, we tested two hypotheses concerning the function of the display and the context in which it is given: 1) cooperation between the partners aimed at stimulating the female for mating, and 2) a signal of male quality used by the female when male and female interests over mating potentially conflict. Under the first hypothesis, sedentary, virgin females that wait in their nest for the arrival of conspecific males must be physiologically stimulated before they are ready to mate (Robinson & Robinson 1980; Suter & Renkes 1984). The courtship display may provide the trigger that sexually primes the female (Platnick 1971; Robinson 1982; Anava & Lubin 1993). This hypothesis predicts that the male courts the female until she signals her willingness to mate, and only upon receiving this message will the male enter the female's nest and attempt to copulate. According to the alternative hypothesis of conflict over mating, information provided by the male during his display enables the female to arrive at a decision whether to allow him to continue courting and later to copulate (e.g., Bukowski & Christenson 1997). This hypothesis predicts that a choosy virgin female should demand a lengthy courtship, while the male will attempt to reduce the effort he puts into courtship in order to lower the energetic cost of the display. The courtship display of many spider species consists of lengthy vibratory signaling before contact is made with the female (Robinson & Robinson 1980; Barth 1990; Arnqvist 1992; Robertson & Adler 1994), and male spiders may advertise their quality using these vibrations (Coyle & O'Shields 1990; Mappes et al. 1996; Parri et al. 1997). Vibrations of the substrate and the vigor of the display may indicate to the female the size of the courting male and his physical condition (e.g., Kotiaho et al. 1996; Rivero et al. 2000; Singer et al. 2000; Maklakov et al. 2003). We conducted experiments in which courtship was interrupted before copulation, and previously courting males or females were then paired with naive (non-courting) mates. By this method, we could compare the behavior of males to naive, virgin females and to females presumed to have been sexually stimulated. The specific predictions for each of the two hypotheses are described below.

METHODS

We collected juvenile and subadult widow spiders, *L. pallidus* from sites around Beer Sheva in July–October, 1998; March–April and June–August, 1999; and June–August, 2000 and 2001. Spiders were taken into the laboratory at the Sede Boqer Campus of Ben-Gurion University, Israel, and kept at 26–28° C, approximately 30% relative humidity and a 10:14 light:dark cycle, similar to the prevailing hours of light and dark for the time of year (March–April). Females were housed in plexiglas cages ($15 \times 30 \times 20$ cm) with thin branches placed in one corner, on which the nest and web were constructed. We fed the females twice a week with nymphs of either locusts (*Locusta* sp.) or crickets (*Acheta domestica*) and fed the males once a week with either first instar locusts or adult fruit flies (*Drosophila melanogaster*). We conducted all experiments after the females had rebuilt their nests and molted to adulthood. Recently molted virgin males and females were selected at random with respect to body size.

In order to determine which of the hypotheses, cooperation or conflict between the sexes, better explains the courtship display we first documented courtship in *L. pallidus*, which had not been described previously.

Male courtship display.—We placed *L. pallidus* males ($n = 28$) individually on the cage inner wall near the capture webs of conspecific virgin females during the morning hours. Observations were begun when the male moved onto the female's web and lasted for two hours or less if the male entered the female's nest, climbed onto the dorsal side of her abdomen, and then moved to the ventral side into a mating position. We defined the behavioral patterns of the display, and recorded the sequence and starting time of each pattern, for each of the males as well as the response of the courted female. We noted the starting time of each behavioral pattern, rather than its duration, because the behaviors were often performed intermittently and short bouts of different components alternated with one another. The time when a male climbed onto the dorsal side of the female's abdomen we designated as the "commitment step"; after this step, 96.4% of the males copulated successfully.

Testing the hypotheses: cooperation versus conflict of interest.— According to the *cooperation hypothesis*, the male's display is aimed at stimulating the female. Thus, the female is expected to signal to the male (e.g., by behavioral or pheromonal cues) when she is ready to mate, and the courting male is expected to respond by entering the nest, mounting the female and copulating. The *conflict of interest hypothesis* suggests that the display provides the female with information about male quality. Thus, the female imposes an energetically costly display on the male as a test of his quality or physical condition. Under this hypothesis, the female is expected to reject males that do not display or whose display is in some way inadequate.

Rejection of a male by the female involves plucking or jerking the web and even chasing the male from the nest entrance. Acceptance of a male, however, does not usually involve an overt behavior. Therefore, we used the response of the male as an indication of a female signal to go on to the next behavioral pattern in the display.

In the following (i–iii) experiments we used males and females collected as juveniles during 1998–1999. In experiment (iv) we used males and females collected during 2000–2001. In all experiments, a virgin male was placed on the inner wall of the cage containing an adult female with her nest and capture web. We observed the pair for three hours or until the male mounted the female's abdomen, and we recorded the times from the start of the courtship until the male a) entered the female nest and b) reached the female abdomen. We conducted three experiments (i–iii) with virgin males and females, in which males and females were either naive, or had already engaged in courtship (experienced). The fourth experiment (iv) compared the behavior of virgin males to virgin or mated females.

We compared durations until the male entered the female's nest (duration of courtship on the web) and until he mounted the female's abdomen (total courtship duration) for the first three tests (i–iii) described below, and used Tukey's post hoc test for pairwise comparisons of mean durations. The data were tested for normal distribution (Liliefors test of the residuals, Systat 10, 2000). ANOVA was used to test for differences among the means for data that were distributed

normally, and Kruskal-Wallis test for data that were not normally distributed. In the fourth experiment (iv) we used a Mann-Whitney U test to compare the response of males to virgin and mated females.

(*i*) *Naive males and naive females*: The courtship of this species is undescribed, so we observed the courtship duration of naive males placed with naive virgin females ($n = 20$). These data serve as a baseline against which we compare the duration of male displays in the subsequent experiments.

(*ii*) *Naive males and experienced females*: In order to test the likelihood that a signal is transferred from a stimulated female to a courting male, we placed a naive *L. pallidus* male onto a web of a female who was courted, but not mated, by a previous male ("stimulated" female) ($n = 11$). The time between removal of the first male at the commitment step and introducing the second, naive male to the female was < 2 min. Following the cooperation hypothesis, the naive courting male is expected to receive an acceptance signal from the already-stimulated female. He should thus reduce his courtship effort and enter the nest after only a short display. Following the conflict hypothesis, the female should accept the new male only after a full display on the web; the naive male should be unaware that the female was courted previously and therefore will perform the full display. However, since this imposed scenario is not likely to occur often in nature, a female may mistakenly perceive the second male courtship as an extension of the first male's display. In this case the female is expected to be less aggressive, and the male may subsequently reduce his display, which may result in an intermediate display time.

(*iii*) *Experienced males and naive females*: In order to test the two hypotheses further, we observed the display of a previously courting male presented with a naive female ($n = 10$). As in the previous experiment, < 2 min lapsed between removing the male and presenting him to a naive female. The cooperation hypothesis predicts that a male encountering a non-stimulated female will start a new, lengthy courting display. The conflict hypothesis predicts that a male that has already courted a female, and thus provided information regarding his quality, will cut short his display. The naive female, however, is expected to reject the male until he performs a full display on her web.

(*iv*) *Naive males and mated females*: We compared the courtship duration of naive males presented with mated ($n = 20$) and with virgin ($n = 27$) females. The spiders were observed for three hours. Males were removed from the cage after climbing on the female abdomen, and the time was recorded. A week before the experiment, males were left with females for 24 h in order to obtain mated females. We regarded the female as having mated if, two months later, at least one egg sac was constructed and the spiderlings hatched. The cooperation hypothesis predicts that a male will display similarly to a mated or a virgin female, since physical stimulation is required by the female, independent of her mating status, before mating can take place. Assuming first-male sperm priority (Austad 1984; Segev et al. 2003), the conflict hypothesis predicts that virgin females should be choosier than mated females, forcing the males to perform a lengthy display.

The predictions of the two hypotheses for each experiment are summarized in Table 1.

Table 1.—Predicted behavior of males in four experiments for each of the two hypotheses proposed: I. Cooperation (mutual stimulation), II. Conflict and female choice for male quality.

	Test	I. Cooperation	II. Conflict
i)	Naive male and naive female	Display	Display
ii)	Naive male and experienced female	Reduce display	Display
iii)	Experienced male and naive female	Display	Reduced display
iv)	Naive male and mated female	Display	Reduced display

RESULTS

The courtship display.—The courtship display of *L. pallidus* males is similar to other *Latrodectus* species (Kaston 1970; Anava & Lubin 1993). The entire courtship is exceedingly long: of 28 *L. pallidus* males observed courting virgin females, only 19 completed the courtship display on the web and entered the nest in less than two hours (mean $\pm$ SD, 109.21 ± 19.07 min).

Most of the display took place on the web, before entering the nest. The final display was performed inside the nest before copulation. The courtship on the female's web consisted of a series of complex movements performed in a specific order (Fig. 1). The male entered the female's web via the frame threads and proceeded to walk on the web, while laying his own dragline threads and disconnecting the lines of the female's web. He cut the thick attachment lines to the substrate, the sticky threads attached to the ground, as well as the threads of the platform and barrier web, and wrapped the web silk into small bundles, which he suspended from the female's threads, usually near her nest (web-reduction behavior: Watson 1986; Anava & Lubin 1993). Finally, he performed small and rapid movements (jerking and abdomen vibrations) on the female's web before entering the nest, followed by climbing on the dorsal side of the female's abdomen and then moving to her ventral side. Jerking movements were sometimes performed inside the nest as well, just before the male climbed on the female's abdomen to attempt copulation. While on the female's ventral side, the male drummed with his pedipalps on and near the female's genital openings (epigynum), and finally inserted a pedipalp into the female genital opening. A female might chase the male
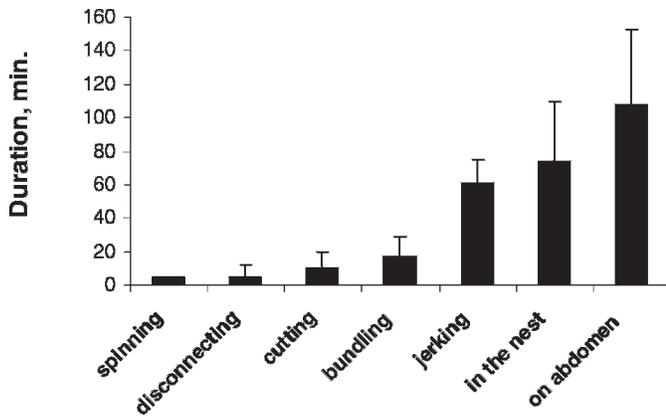
Figure 1.—The sequences of behaviors constituting the courtship display of male widow spiders *Latrodectus pallidus* ($n = 19$). Shown are mean $\pm$ SD of the first occurrence (in minutes from the start of the display) of each behavior component. Note that some components were performed in alternation (e.g., disconnecting capture-web threads, cutting of frame threads and bundling of threads). "On abdomen" refers to climbing onto the dorsal side of the female's abdomen.

Figure 2.—Durations (mean $\pm$ SD) of male courtship on the web until entering the female's nest (black bars) and of the total courtship display until the commitment step (white bars) for each of the four tests.

away at various stages, and the male would then resume courting on the web, outside the nest. Once the male was on the female's abdomen, however, copulation usually followed. We referred to the male mounting the female's abdomen as the *commitment step*, and in the following analyses we have taken this step as an indication of the female's acceptance of the courting male.

Cooperation versus conflict of interest hypotheses.—*Duration of courtship on the web:* The durations of male courtship prior to entering the female's nest were not normally distributed. The display time before entering the female's nest differed significantly among the four tests (Kruskal-Wallis test: $H = 21.601$, $P < 0.001$, $n = 38$). In each of the different experiments, some males did not enter the nest within three hours or did not reach the commitment step during the observation time. These males, fewer than 20% of each experiment, were excluded from the statistical analyses.

Naive males that courted naive females (i) ($n = 18$), displayed for 77.67 ± 39.91 min (mean $\pm$ SD) before entering the nest. Naive males that were placed in cages of virgin females that had been courted previously by another male (ii) ($n = 10$), displayed for 68.80 ± 26.26 min before first entering the nest. All males ($n = 10$) that were transferred to cages of naive females after reaching the commitment step in the nest of another female (iii) immediately attempted to enter the second female's nest (display duration 3.0 ± 1.94 min), and all were chased away by the female.

Total courtship duration: There was no significant difference among the different experiments in overall courtship time until reaching the commitment step on the female's abdomen (ANOVA: $F_{2,28} = 2.862$, $P = 0.08$). Naive males that courted naive females (i) ($n = 16$), reached the commitment step after a total display duration of 101.73 ± 23.55 min. When paired with previously courted virgin females (ii) ($n = 8$), the display duration of naive *L. pallidus* males until the commitment step, was 72.5 ± 16.66 min. Virgin males that had previously courted an experienced female and were then placed in a cage with a naive female (iii) were chased out of the nest by the
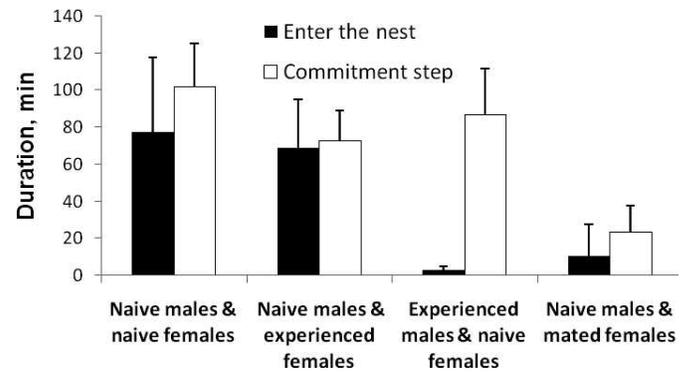
female when they first tried to enter the female's nest. One of these rejected males did not resume courting, and an additional male did not reach the commitment step within three hours. All other males ($n = 8$) resumed courting on the web and repeated all behavioral patterns in the normal order (Fig. 1). For these males, courtship duration until the commitment step was 86.57 ± 24.91 min.

Virgin males tested with mated females (iv) did not cut the thick attachment threads of the female's web or bundle them in front of her nest. Instead they briefly laid dragline silk on the female's web, cut some of the thin web threads and rapidly entered the female's nest and climbed on the her abdomen, jerking briefly just before entering the nest (duration until entering the nest 10.41 ± 17.38 min, until commitment step 23.33 ± 14.62, $n = 15$). Naive males courting virgin females ($n = 21$) performed the typical courtship sequence until entering the female nest (60.05 ± 33.1 min) and reached the female's abdomen (90.7 ± 35.6 min) after a significantly longer time (Mann-Whitney U test: $U = 284.5$, $n = 36$, $P < 0.001$ and $U = 308.0$, $n = 36$, $P < 0.001$, respectively). The duration of the courtship display of males in all of the experiments are summarized in Fig. 2.

DISCUSSION

The results of the experimental manipulation of male and female experience suggest that the male's courtship display is better explained by the hypothesis of conflict over mating interests between the sexes than that of male and female cooperation to sexually stimulate the female. We discuss the two hypotheses suggested in the light of our results.

Cooperation.—In some spider species, the female signals her acceptance by adopting a receptive posture (Robinson & Robinson 1980), whereas in others females indicate receptivity by remaining stationary (Forster 1982). In the widow spider *L. pallidus*, the females draw away from the nest wall towards its center, allowing the male the space needed to approach the ventral side of her abdomen. Testing the hypothesis of cooperation aimed at stimulating the female, we predicted that females that were previously stimulated would signal their readiness to mate. Upon perceiving the signal, a male should respond by ceasing his display and entering the nest. However, we found that males did not change their display when they encountered previously courted females (test ii). Apparently,

they did not identify these females as receptive, and their courtship duration was not statistically different from that of males courting naive females (test i). In addition, a male that was interrupted during his display at the commitment step and then transferred to a cage with a naive female (iii) immediately attempted to enter the female's nest and proceed with his display from the point at which it was interrupted. Thus, we suggest that the male failed to receive a signal from the female indicating that she was not stimulated to mate. Finally, if courting functions to stimulate the female physically before mating, previously mated females presented with a male several days after their first mating should not differ from virgins in requiring a stimulating courtship display. Contrary to this prediction, however, we found that males shortened their display when they encountered mated females.

Conflict over mating interests.—The courtship display of the male widow spider *L. pallidus* is lengthy and consists of behaviors such as web vibration (jerking) and cutting and bundling of silk that are likely to be energetically costly. The entire process may take more than two hours before the male enters the nest and a total of four or more hours before he copulates with the female (A.R. Harari, personal observation). At each stage of the display, females may gain information concerning the male's quality.

Our experiments revealed that virgin females prevented males from mounting and copulating if the males had not performed all parts of the display, and naive males courted virgin females regardless the female's previous experience. These results suggest that males expect to be accepted by females only after displaying the full courtship, and that a female accepts a male only after he completes a full display on her web. We tested both sides of the coin by observing whether a naive male courted a female immediately after she had been courted by a previous male up to the commitment step (ii). In this experiment, males engaged in the full courtship display, suggesting that they did not receive any cue from the female. In the reciprocal experiment (iii), a naive female was courted by a male whose courtship with a different female was interrupted at the point of entering her nest. The male's response, to continue from the point that he had stopped, suggests, again, that he initially received no cue from the female. The female's aggressive response, however, suggests that she had not had an opportunity to assess the male's quality and therefore rejected his attempt to enter the nest. Overall, we interpret our results as indicating that the male's display is under female control, such that males that attempt to shorten the display are prevented by virgin females from proceeding with close-range courtship inside the nest, mounting and copulation.

Additional support for the hypothesis of a conflict over mating interests and female control over the length of the male's display comes from the results comparing the male's display to a mated or virgin female. Female widow spiders may mate with more than one male (Anava & Lubin 1993; Andrade 1996; Segev et al. 2003; Segoli et al. 2006). We found that males of *L. pallidus* shortened their display significantly when courting mated females, a behavior that is expected if there is first-male sperm priority, and thus, a lower probability of fathering the offspring from a second or later mating. Segev et al. (2003) showed evidence for first-male sperm priority in *L. revivensis*, as is the case in many other entelegyne spider species that have been tested (Christenson & Cohn 1988; Watson &

Lighton 1994; Singer & Reichert 1995; Snow & Andrade 2005, but see e.g., Schneider at al. 2000 for a case of mixed paternity). In *L. pallidus* (Segoli et al. 2006) as well as in other *Latrodectus* species (Levi 1959; Bhatnagar & Rempel 1962; Kaston 1970; Foelix 1996; Berendonck and Greven 2002; Snow et al. 2006; Segoli et al. 2008), the tip of the male's embolus is often broken during copulation and becomes lodged in the insemination duct or inside the spermatheca. The presence of the broken embolus tip may act as a mating plug and may reduce the likelihood that a second male will successfully inseminate the female (Berendonck & Greven 2002; Segoli et al. 2008). Thus, if the first male is accepted only after a stringent test and the contribution of the second male to the clutch is limited, a mated female may be less choosy with subsequent males. Accepting a second male with little courtship could be a bet-hedging strategy, as suggested for *Neriene litigiosa* (Keyserling 1886) (Linyphiidae) by Watson (1991b).

Our results indicate that males are able to distinguish between virgin and mated females (as shown in *L. hasselti*, Stoltz et al. 2007) and reduce their display effort to the latter. Pheromones produced by the female have been shown to play an important role in mate attraction (e.g., *L. revivensis*: Anava & Lubin 1993) and may also provide a means of assessing female reproductive state on the web (Papke et al. 2001). However, it will always be advantageous for males to shorten the display duration and reduce its cost if the female will allow it. In courting virgin females, males frequently attempt to enter the nest and are repeatedly chased off by the female to continue their display on the web. This behavior suggests that males repeatedly test the female's aggressive intentions during courtship; virgin females reject males that have not met a criterion, whereas mated females accept a second male more readily.

In conclusion, our experiments suggest that the costly display of the widow spider *L. pallidus* is unlikely to function as physical stimulation of the female to mate. Rather, the courtship display in this species is likely a result of a conflict of interests, with the female imposing a long, vigorous and energetically costly display in order to test the male's quality.

In recent years, the view of reproduction as a cooperative effort has been challenged by increasing evidence for conflicting interests between the sexes (Dawkins 1976; Parker 1979; Holland and Rice 1998; Zeh and Zeh 2003). Although both parents share an interest in maximizing the fitness of their offspring, they often have conflicting interests in the amount of reproductive effort (Parker 1979). This conflict begins with the investment in the size of male and female gametes (anisogamy, Trivers 1972) and continues with the conflict over the number of matings (Bateman 1948). As a consequence, females are expected to be choosy, selecting some males and rejecting others based on their phenotypic traits (Andersson 1994; Arnqvist and Rowe 2005). This scenario may lead to the complex and lengthy male display in various spider species, including *L. pallidus* (Kaston 1970; Ross & Smith 1979, Lubin and Anava 1993; Forster 1995). The fixed components observed in the display of *L. pallidus* and other *Latrodectus* species (e.g., Lubin and Anava 1993) can be viewed in the light of the known predatory and cannibalistic nature of the genus (Elgar & Schneider 2004) and may be aimed at appeasing the females by providing cues for species recognition (Ryan 1985; Andersson 1994). The length of the display and its energetic cost, however, may have evolved as

a consequence of female choice for energetically displaying males. The results of our experiments support the latter view.

ACKNOWLEDGMENTS

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