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RESEARCH ARTICLE

COURTSHIP AND REPRODUCTIVE ISOLATION IN TWO CLOSELY RELATED DESID SPIDERS, *BADUMNA LONGINQUA* AND *BADUMNA INSIGNIS* (ARANEIDAE: DESIDAE)

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ABSTRACT

We studied the development and reproductive behavior of two sympatric New Zealand spiders, *Badumna longinqua* and *Badumna insignis* (Araneae: Desidae), in the laboratory. Both species have intersexual size dimorphism and, within each species, males vary up to 35-fold in size. Females of *B. longinqua* produce up to 12 egg sacs, and those of *B. insignis* produce up to 18 sacs. Clutch size and number of egg sacs is positively correlated with adult female longevity, but not female weight, in both species. Courtship in *B. longinqua* is longer and entails more acts than in *B. insignis*. Both species exhibit prolonged copulation. The number of palpal insertions during copulation is not correlated with clutch size, length of sperm storage, female longevity, male weight, or female weight in either species, but number of insertions is positively correlated with relative male weight in *B. longinqua* and time until first oviposition in *B. insignis*. The two species do not interbreed in the laboratory. Although theyare similar morphologically, they are reproductively isolated via reproductive behavior; similarities in courtship suggest that the female might use vibratory or chemical cues to assess conspecificity of males.

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INTRODUCTION

Proposed functions for courtship in spiders include suppression of predatory behavior (Robinson and Robinson, 1978), promotion of mutual arousal or stimulation (Crane, 1949), synchronization of mates (Platnick, 1971), opportunities for species recognition (Stratton and Uetz, 1981), facilitation of male assessment of female virginity (Suter, 1990), and orientation of the spiders (Platnick, 1971). Courtship has also been viewed as a reproductive isolating mechanism. The traditional view of courtship as precopulatory behavior has been expanded to include a number of aspects of actual copulation, with many spiders engaging in copulatory courtship (Eberhard 1994; Eberhard and Huber, 1998). Courtship and mating behavior have been widely studied in spiders (e.g., Robinson, 1982; Bukowski and Christenson, 1997). Here we present one of the few comparative studies of reproductive behavior in two closely related species of spiders, providing an opportunity to examine the evolution of courtship behaviors and reproductive isolating mechanisms. *Badumna longinqua* (L. Koch) and *B. insignis* (L. Koch) are common, morphologically similar New Zealand spiders of the family Desidae, possibly introduced from Australia (Forster, 1970; as *Ixeuticus martius* and *I. robustus* respectively). Both species construct funnel retreats, often adjacent to one another in crevices, and surround the retreats with cribellate sheet webs. We examined the components of reproductive behavior of these two species to determine 1) the possible adaptive significance of selected courtship and mating behaviors, 2) the extent of reproductive isolation, and 3) if courtship behaviors might have evolved to reduce hybridization, that is, in the context of reproductive isolation. Understanding the relation of fitness characters, such as fecundity, to courtship features can provide insight into the evolution of reproductive behavior.

MATERIALS AND METHODS

Rearing conditions: Gravid females of *B. longinqua* and *B. insignis* were collected from crevices on buildings at the University of Canterbury, Christchurch, New Zealand. F1 and F2 progeny of these females were used in experiments. Throughout the study, spiders were maintained in an environmental chamber (26 ± 2 °C, 65 ± 4% relative humidity, 14L:10D photoperiod) in Clemson, SC. They were reared in containers 5.5 cm high x 9.5 cm diameter, each with a moist cotton ball. All spiders were fed twice per week on the same diet (German cockroaches, tachinid flies, house flies, drosophilid flies, and diamondback moths). Spiders used in developmental studies were reared individually from the day they emerged from the egg sac until their final molt. All other spiders were separated into groups of five siblings and reared together for up to a month, at which time 16 individuals were chosen randomly from each clutch and reared separately. If a clutch contained 30 or fewer individuals, all individuals were reared. No spider was ever used more than once unless a female did not mate; that female could then be used in another mating trial.

Development and fecundity: For each spiderling, we recorded the duration of each post-emergence instar by examining containers daily for exuviae. We determined the number of days to reach maturity for individually reared males and females of *B. longiqua* and *B. insignis*. We also weighed each male within 24 h of the final molt to test the hypothesis that heavier males required longer to mature. Females were weighed on the day of mating because their weight varied during egg development. Both weight and carapace width have been used as indicators of spider size (Hagstrum, 1971). Since weight can vary within an instar, we also measured carapace width of adult spiders and analyzed data for possible correlation between weight and the sclerotized carapace which remains constant in size within an instar. To determine the reproductive capacity of each species, we mated virgin females with virgin males and collected all egg sacs. We removed females from each of their successive egg sacs within 12 h of egg sac construction. We recorded the date of egg-sac construction, clutch size (eggs and spiderlings), and date of the first spiderling emergence from each egg sac. Normally distributed data were analyzed with Analysis of Variance (F), and non-normal data or data with uneven sample sizes were analyzed with Kruskal-Wallis (H) (Zar, 1984). The LSMeans procedure and the Tukey type multiple comparison test were used to identify significantly different means. Sample sizes less than five were not entered into analyses. All means are reported with their standard errors. Voucher specimens of each species are deposited in the Clemson University Arthropod Collection.

Courtship and mating behavior: We mated 35 virgin pairs of each species. Pairs were composed of non-sibling spiders matched by age (measured from the last molt to the date of pairing). Observations, made through a 4x magnifying lens fitted with a ring light, began with the introduction of a male onto the edge of a female's web, continued through courtship and mating, and ended when the male moved away from the female by 5 cm or more. For both species, we transcribed behavioral acts into a first-order preceding-following transition matrix and calculated expected values and standard normal deviates for individual transitions. We used a binomial test to analyze the standard normal deviates and determine which transitions occurred at a frequency greater than expected by chance (Bishop *et al.,* 1975; Fagen and Young, 1978). We then constructed a flow diagram for each species on the basis of significant transitions ($P < 0.01$). For each species, we used correlation analysis to evaluate the relation between the number of palpal insertions (a measure of copulation duration) and the following reproductive characters: duration of copulation; length of sperm storage (determined by production of the last fertile eggs); female longevity; number of eggs and number of spiderlings in the first egg sac, the first five egg sacs, and all egg sacs; total number of egg sacs; time from mating to oviposition of the first clutch; female weight; male weight; and relative male weight [(male weight/female weight) x 100] of mated individuals. Using a Student's t-test on paired data, we compared the number of insertions by the right versus the left palp during copulation. Males of each species (n = 11 trials/species) were given a choice between a mated and an unmated female. The three spiders in each trial were the same age (measured from the last molt). We alternated which web (that of a virgin female [n = 5 for *B. longinqua*, n = 6 for *B. insignis*] or that of a mated female [n = 6 for *B. longinqua*, n = 5 for *B. insignis*]) was used for testing, and we introduced males equidistant from the two females. We observed the spiders for 1 hour.

Interspecific pairings: Reciprocal species pairings were made by introducing males of *B. insignis* onto the edge of *B. longinqua* female webs (n = 30), and males of *B. longinqua* onto the edge of *B. insignis* female webs (n = 20). Each pair was observed for 1 hour, and all behaviors and interactions were recorded.

RESULTS

Development and Fecundity: Males of *B. longinqua* required five (50.0%) or six (50.0%) molts to reach maturity, whereas females required six (60.0%), seven (30.0%), or eight (10.0%) (Table 1). Males of *B. insignis* required three (93.8%) or four (6.2%) molts, whereas females required seven (76.9%) or eight (23.1%). The length of the intermolt interval typically increased with each molt in males and females of both species (Table 1). Cephalothorax width was significantly correlated ($P< 0.001$) with weight in *B. longinqua* and *B. insignis* males and females (Table 2); therefore, weight was used as a measure of size in subsequent experiments. The means for six life-history characters are summarized (Table 3) with ranges given in text where applicable. Both species exhibited extreme intersexual size dimorphism in adult weight, with males being especially variable. In both *B. longinqua* (n = 232) and *B. insignis* (n = 538), heavier males required longer to mature than lighter males (r = 0.369, r = 0.533, respectively; $P< 0.001$). Thus, males of both species were smaller on average than females and required less time (d) to mature than females (Table 3). Males of *B. longinqua* (n = 232) weighed 0.0057-0.1184 g and, lthough most males were smaller than females, some were as large as, or larger than, females (Fig. 1). Males of *B. insignis* (n = 538) weighed 0.0013-0.0450 g (Fig. 2)and were generally smaller than females (Fig. 2). Females of both species produced multiple egg sacs; females of *B. longinqua* constructed their first egg sac about one month after mating, whereas those of *B. insignis* constructed their first sac about two and a half weeks after mating (Table 3).

In *B. longinqua*, subsequent intervals between production of consecutive egg sacs varied from 11.4 to 18.8 days and, in *B. insignis*, from 11.0 to 19.0 days. In *B. longinqua*, the number of days from mating to production of the last fertile egg sac (indicating length of sperm storage) ranged from 12 to 175 days (Table 3). In *B. insignis*, the number of days from mating to production of the last fertile egg sac ranged from 15 to 177 days (Table 3). Female longevity, from mating to death, was 24-272 days in *B. longinqua* and 35-212 days in *B. insignis* (Table 3). The maximum number of egg sacs produced by *B. longinqua* and *B. insignis* was 12 and 18, respectively (Table 4). The total number of eggs per sac varied from 8 to 63 in *B. longinqua* and from 10 to 95 in *B. insignis.* In *B. longinqua*, no significant differences occurred among sacs in the number of eggs (F = 1.18, $P = 0.323$), number of progeny (H = 10.99, $P = 0.141$), or total clutch size of consecutive egg sacs (F = 0.340, $P = 0.935$) (Table 4).

Table 1. Days (x ± SE, n) required for development of males and females of *Badumna longinqua* and *Badumna insignis* males and females in the laboratory (26 ± 2^{0}C). Male data of *B. longinqua* were analyzed with Kruskal-Wallis, and female data of *B. longinqua* plus data of *B. insignis* were analyzed with ANOVA. Means within each column followed by different letters are significantly different (*P*< 0.0001; Tukey type multiple comparison test for *B. longinqua* males, and LSMeans procedure for females, Zar [1984]). * = not included in statistical analysis.

Intermolt interval	***Badumna longinqua***		***Badumna insignis***	
	Males	**Females**	**Males**	**Females**
Emergence - Molt 1	4.8 ± 1.42, 12a	4.7 ± 1.18, 10a	6.2 ± 0.39, 16a	4.5 ± 0.35, 13a
Molt 1 - Molt 2	8.5 ± 0.31, 12b	8.0 ± 0.45, 10b	11.1 ± 0.27, 16b	10.3 ± 0.33, 13b
Molt 2 – Molt 3	7.3 ± 0.26, 12a	8.0 ± 0.68, 10b	12.1 ± 1.09, 16b	9.8 ± 0.17, 13b
Molt 3 - Molt 4	7.7 ± 0.28, 12b	8.2 ± 0.85, 10b	10.0	1*
Molt 4 - Molt 5	9.2 ± 0.19, 13b	10.6 ± 0.68, 12b	9.9 ± 0.38, 10b	9.6 ± 0.24, 13b
Molt 5 - Molt 6	10.5 ± 0.62, 6b	13.8 ± 1.06, 10c		12.5 ± 0.42, 13c
Molt 6 - Molt 7	15.8 ± 1.49,	4*	17.5 ± 1.37,	13d
Molt 7 - Molt 8	30.0	1*	21.0 ± 1.156	3*

Table 2. Correlation between cephalothorax width (mm) with weight (g) in *Badumna longinqua* and *Badumna insignis*

	B. longinqua		*B. insignis*	
	Mean	Female	Mean	Female
r	0.901	0.880	0.984	0.844
df	33	29	31	33

Table 3. Life-history characters (x ± SE, n) of *Badumna longinqua* and *Badumna insignis* in the laboratory (26 ± 2^{0}C. NA = not applicable

Life-history Character	***Badumna longinqua***		***Badumna insigni***	
	Males	**Females**	**Males**	**Females**
Adult weight (g)	0.04 ± 0.001, 232	0.12 ± 0.005, 179	0.01 ± 2.394E-4, 538	538 0.22 ± 0.009, 112
Maturation time (d)	73.7 ± 1.05, 232	97.7 ± 1.16, 211	47.6 ± 0.66, 538	107.3 ± 0.89, 382
Number of egg sacs	NA	4.9 ± 0.86, 17	NA	5.7 ± 1.49, 11
Mating to first sac (d)	NA	27.8 ± 6.09, 20	NA	17.1 ± 1.22, 11
Mating to last fertile sac (d)	NA	86.3 ± 16.69, 11	NA	86.9 ± 20.62, 8
Female longevity (d)	NA	114.0 ± 14.60, 22	NA	100.1 ± 16.96, 11

Table 4. Clutch sizes (eggs + spiderlings) (x ± SE) of consecutive egg sacs constructed by *Badumna longinqua* and *Badumna insignis* in the laboratory (26 ± 2^{0}C). * = not included in ANOVA.

Egg sac Number	***Badumna longinqua***		***Badumna insignis***	
	Clutch size	**n**	**Clutch size**	**n**
Sac 1	54.4 ± 5.87	20	54.8 ± 5.04	11
Sac 2	51.3 ± 4.87	18	67.0 ± 4.81	9
Sac 3	56.9 ± 3.49	10	48.4 ± 6.95	7
Sac 4	58.4 ± 9.67	10	49.3 ± 6.37	7
Sac 5	59.0 ± 6.37	7	40.7 ± 7.72	7
Sac 6	45.3 ± 8.07	7	46.2 ± 8.07	4*
Sac 7	52.2 ± 3.89	5	51.0 ± 15.00	2*
Sac 8	53.2 ± 6.43	5	42.5 ± 18.50	2*
Sac 9	32.8 ± 10.77	4*	35.0 ± 8.00	2*
Sac 10	43.5 ± 1.50	2*	34.5 ± 7.50	2*
Sac 11	63.0	1*	36.5 ± 3.50	2*
Sac 12	8.0	1*	51.0	1*
Sac 13			30.0	1*
Sac 14			39.0	1*
Sac 15			32.0	1*
Sac 16			95.0	1*
Sac 17			10.0	1*
Sac 18			40.0	1*

Likewise, in *B. insignis*, no significant differences occurred among sacs in the number of eggs (H = 2.26, P = 0.688), number of progeny ((F = 0.39, *P* = 0.818), or total clutch size (F = 2.61, *P* = 0.052) (Table 4). The time for spiderlings to emerge from consecutive egg sacs in both species ranged from 16.2 to 29.0 days and was not significantly different in either species. Female weight in *B. longinqua* was not correlated with the total number of egg sacs (r = 0.048, df = 15, *P*> 0.05), total number of undeveloped eggs (r = 0.019, df = 13, *P*> 0.05), or total number of progeny (embryonated eggs plus spiderlings) (r = 0.007, df = 13, *P*< 0.05). However, female longevity (post-mating) was correlated with the total number of egg sacs (r = 0.766, df = 15, *P*< 0.001) and total clutch size (undeveloped eggs plus embryonated eggs plus spiderlings) (r = 0.746, df = 13, *P*< 0.002). Female weight of *B. insignis* was not correlated with the total number of egg sacs (r = 0.421, df = 9, *P*> 0.05), total number of undeveloped eggs (r = 0.149, df = 7, *P* > 0.05), or total number of progeny (r = 0.621, df = 7, *P* > 0.05). However, female longevity (post-mating) was correlated with the total number of egg sacs (r = 0.923, df = 9, *P* < 0.001) and total clutch size (r = 0.936, df = 6, *P* < 0.001).

Precopulatory Behavior: *Badumna longinqua* had 13 behavioral acts associated with courtship (Fig. 3), and *B. insignis* had 11 (Fig. 4). Males performed nearly all visible courtship acts. Females were passive throughout courtship, except when they attacked males. In about 15% of the pairs, females of *B. longinqua* pushed males away with their legs; one female initiated leg contact with the male. One female of *B. insignis* vibrated its abdomen, and females in about 15% of the pairs moved their legs or moved in the web, causing males to retreat and pluck.

Table 5. Correlations between number of palpal insertions (r, n) and fitness characters in *Badumna longinqua* and *Badumna insignis* in the laboratory (26 ± 2 ^{o}C). Except where specified, $P > 0.05$.

Fitness Character	*Badumna longinqua*	*Badumna insignis*
Female longevity	0.058, 22	0.032, 11
Number of eggs in first sac	0.322, 20	-0.215, 11
Number of progeny in first sac	-0.245, 20	0.173, 11
Number of eggs in first five sacs	-0.125, 7	-0.182, 5
Number of progeny in first five sacs	-0.289, 13	0.183, 5
Total number of eggs	0.054, 15	0.436, 9
Total number of progeny	0.229, 15	0.430, 9
Total number of egg sacs	-0.014, 17	0.209, 11
Number of days to first oviposition	0.318, 20	-0.470, 11, $P < 0.05$
Male weight	0.311, 35	-0.069, 35
Female weight	-0.256, 35	0.162, 35
Relative male weight	0.435, 35, $P < 0.01$	-0.181, 35

The following eight behavioral acts were shared by both species:

1. **Leg contact:** Legs I and/or II of the male contact the body or legs of the female.
2. **Climb on female dorsum:** The male approaches the female from the front, climbing over the cephalothorax to the abdomen. In fewer than 20% of pairs, males of *B. longinqua* climbed directly on the female abdomen from behind. The smaller males of *B. insignis* climbed the front legs of the female to reach the cephalothorax.
3. **Vibrate palps:** The male vibrates his palps in a vertical plane. Males of *B. longinqua* vibrate their palps on the web or on the female. Those of *B. insignis* generally (> 90% of pairs) vibrate the palps on the female legs, carapace, or abdomen.
4. **Deposit silk:** While moving on the web, the male deposits silk on the web. The male of *B. longinqua*, but not of *B. insignis*, also deposits silk on the female's body.
5. **Cut silk:** The male cuts the silk of the female's web, and in more than half of the cases, it is performed in combination with the deposition of silk.
6. **Pluck silk:** The male pulls back on silk with his front legs and then releases it. The male of *B. longinqua* also plucks silk with its palps. This behavior is performed while stationary or as the male moves through the web.
7. **Cross over:** After inserting the palp repeatedly on one side of the female, the male crosses over the female's dorsum and positions himself to mate on the opposite side of the female. Cross over was seen in only four males of *B. insignis* but was observed in all males of *B. longinqua*. As the male crosses over the female’s dorsum, he vibrates his palps on the female and vibrates its abdomen. One male of *B. longinqua* deposited silk on the female as he crossed over.
8. **Mate:** The male begins to insert his palps.

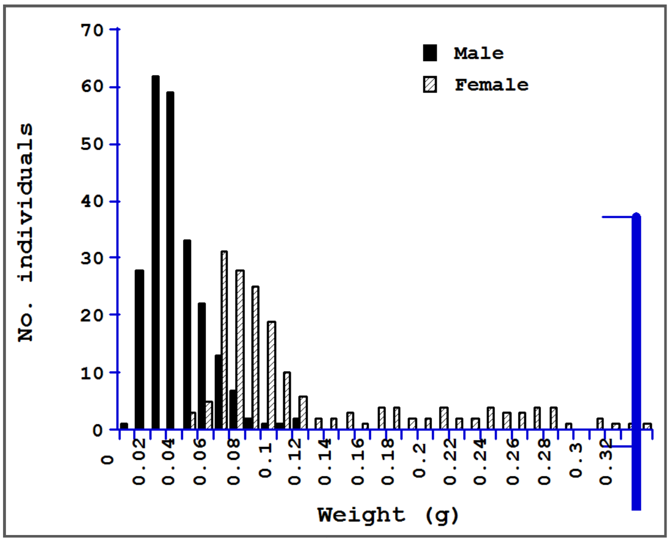

Figure 1. Weight distribution of adult males and females of *Badumna longinqua*in the laboratory (26 ± 2 ^{o}C)

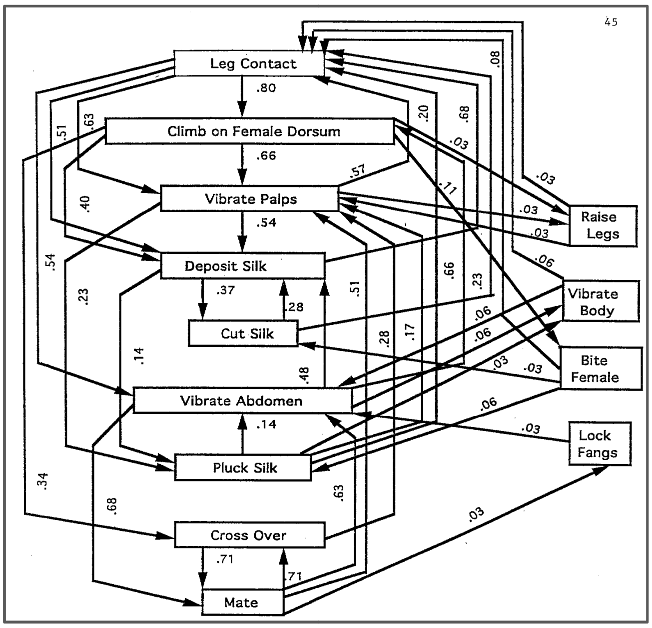

Figure 3. Flow diagram of courtship acts for *Badumna longinqua*, showing significant ($P < 0.01$) behavioral transitions. Values indicate frequency of 35 pairs showing a specific transition

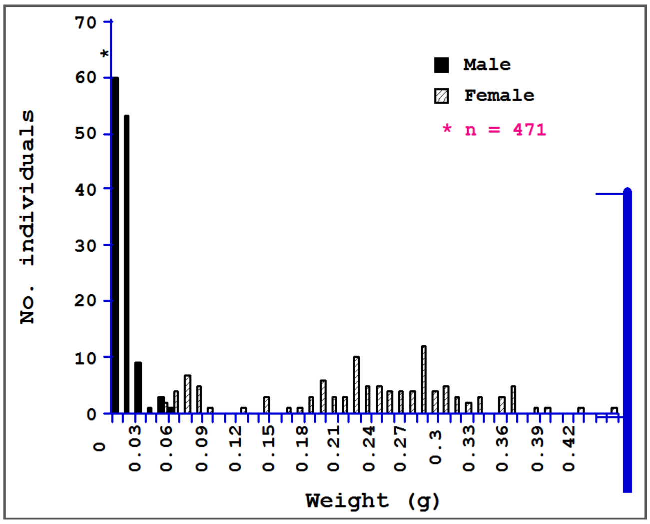

Figure 2. Weight distribution of adult males and females of *Badumna insignis*ins the laboratory (26 ± 2 ^{o}C)

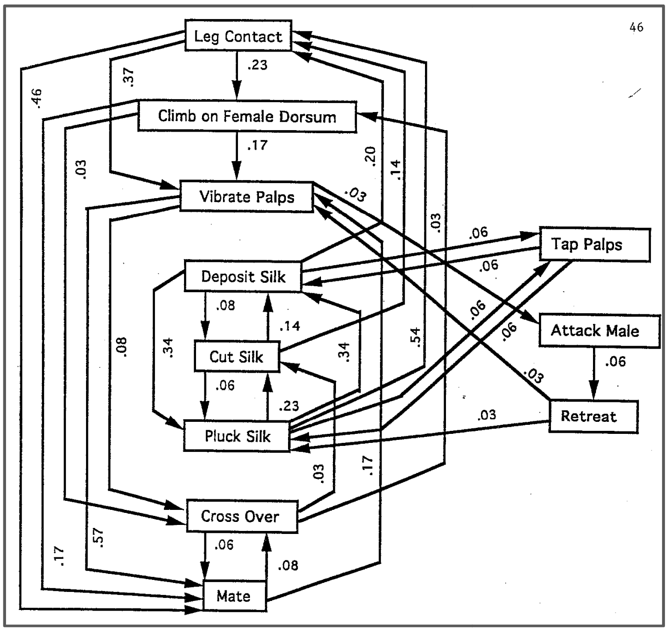

Figure 4. Flow diagram of courtship acts for *Badumna insignis*, showing significant (*P*< 0.01) behavioral transitions. Values indicate frequency of 35 pairs showing a specific transition.

The following behaviors were exhibited only by *B. longinqua*:

1. Vibrate abdomen: The male vibrates his abdomen up and down on the web or on the female.
2. Raise legs: The male raises his front pair of legs so that the femora are straight up and the distal parts of the legs extend from the femora at a 90° angle.
3. Vibrate body: The male vibrates his legs, cephalothorax, and abdomen in a vertical plane.
4. Bite female: After climbing on the female dorsum, the male nips the female. This behavior is followed by the female retreating. No hemolymph was detected on females after being nipped.
5. Lock fangs: The male locks his fangs with those of the female.

The following behaviors were exhibited only by *B. insignis*:

1. Tap palps: The male alternately lifts and lowers his palps; the movement is slower than the behavior 'vibrate palps'.
2. Attack male: The female lunges at, chases, or seizes and eats the male. Males of both species were attacked, but the behavior appears on the flow diagram only when it occurs before mating because the flow diagram terminates with the end of mating.
3. Retreat: The male moves away from the female.

Copulatory Behavior: Males of *B. longinqua* (n = 35) inserted their palps 1-322 times (mean = 101.9 ± 18.71), with no significant difference in the number of insertions by the left palp (n = 1725 insertions) versus the right palp (n = 1746 insertions) (t = 0.47, *P* = 0.642). Males inserted the left palp while on the left side of the female and the right palp while on the right side. Mating lasted 0.54-241.53 min (n = 33). During mating, spiders faced opposite directions, dorsal side up, and males ranged from being parallel to the female to being at a 90° angle. Two males were killed by females during mating, and three males were attacked during mating but escaped. Four additional males were attacked after mating when they approached females and continued courtship. Two males escaped after losing legs. Males of *B. insignis* (n = 35) inserted their palps 1-13 times (mean = 2.8 ± 0.53), with no significant difference in the number of insertions by the left palp (n = 56 insertions) versus the right palp (n = 41 insertions) (t = 1.077, *P* = 0.289). Mating lasted 0.20-32.78 min (n = 22). Males and females mated in the same position as those of *B. longinqua*. Additionally, males mated under the female, venter to venter, and did not cross over before switching palps. Nine males of *B. insignis* were attacked and eaten by females during mating, and one male was attacked during mating but escaped. One male was attacked, and one was killed after mating.

The mean number of insertions was 4.1 for the 10 males killed, and 2.3 for the 24 not killed. In *B. longinqua* (n = 33), copulation duration ranged from 0.54 min to 241.53 min, and in *B. insignis* (n = 22), copulation duration ranged from 0.20 min to 32.78 min. Copulation duration was correlated significantly with the number of palpal insertions in both *B. longinqua* (r = 0.874, df = 31, *P*< 0.001) and *B. insignis* (r = 0.605, df = 20, *P*< 0.05). However, the length of viable sperm storage (i.e., days from mating to production of the last fertile egg sac) was not correlated significantly with the number of palpal insertions for *B. longinqua* (r = 0.436, df = 11, *P*> 0.05) or *B. insignis* (r = -0.052, df = 6, *P*> 0.05). In *B. longinqua* (n = 11) sperm storage ranged from 12 to 175 days, with an average of 86.3 ± 16.69 days. In *B. insignis* (n = 8), sperm storage ranged from 15 to 177 days, with an average of 86.9 ± 20.62 days. Of 12 fitness characters examined in each species, only one in each species was correlated significantly with the number of palpal insertions (Table 5). In *B. longinqua*, the number of palpal insertions was correlated with relative male weight (*P*< 0.01), and in *B. insignis*, the number of days to first oviposition was correlated with the number of palpal insertions (*P*< 0.05). In trials involving a choice between virgin and mated females, males of *B. longinqua* mated with virgin females in two trials (18.2%) and mated females in three trials (27.3%). In six trials (54.5%), the male did not mate with either female, possibly because the females were involved in agonistic interactions with one another. Males of *B. insignis* mated with virgin females in 10 trials (90.9%) and a mated female in one trial (9.1%).

Interspecific Pairings: When males of *B. insignis* entered webs of *B. longinqua* females, males ceased movement or moved through the web without exhibiting their typical courtship sequence; fewer than half of the males deposited silk, cut silk, or plucked the web. As males moved in the web, females moved toward them. Males then retreated or ceased movement. Three males (10%) were killed and eaten by females. When males of *B. longinqua* entered webs of *B. insignis* females, they wandered, with less than half of the males cutting or depositing silk. As males moved in the web, females followed them, extending their front legs and vibrating them on the web. When males ceased movement, females continued wandering in the web. Once attacked, males positioned their legs toward, and their bodies away from, females. Five males lost legs when attacked; one male escaped after losing legs. Seven males (35%) were killed and eaten by females.

DISCUSSION

Females of *B. insignis* and *B. longinqua* are generally larger than males and require more molts and time to mature. Although exceptions exist (Willey and Adler, 1991), female spiders typically are larger and require more molts than males (Foelix, 1996). In *B. insignis* and *B. longinqua*, both sexes vary in the number of molts, resulting in different sizes of adults within each sex. Whether this size variation has a genetic basis or is the result of differential food intake, or both, is unknown. The adaptive significance of extreme size dimorphism, similar to that in *B. insignis*, might result from selection through sexual cannibalism (Elgar, 1991). Small males might be ignored as prey by females because of their low nutritional value (Robinson and Robinson 1980). Females of *B. insignis* are cannibalistic during and after mating, and the small size of males might enable them to escape quickly after mating. The tradeoff for small size might be that large males are better competitors for mates (Vollrath, 1980a). Both *B. longinqua* and *B. insignis* can produce at least 12 egg sacs, but the number of sacs and the clutch size are related to female longevity rather than female weight. In some species of spiders, clutch size is related to female size (Wise, 1984; Killebrew and Ford, 1985), but not in other species (Foelix, 1996). The number of egg sacs produced might be constrained by the degree of maternal care. For example, females of *Florinda coccinea*, which exhibit no maternal care beyond egg-sac construction, produce up to 10 sacs in a season (Willey and Adler, 1991), whereas those of *Peucetia viridans*, which guard their egg sacs and spiderlings, produce only one or two egg sacs (Willey and Adler, 1989). In both species of *Badumna*, we removed females from their egg sacs, so we do not know the degree of maternal care; however, we know that spiderlings can emerge from the sacs without maternal assistance. We also have observed females placing prey remains on egg sacs, which might help camouflage the sacs, and have observed spiderlings feeding on prey caught by the female. Females of both *B. insignis* and *B. longinqua* can store sperm for at least 175 days and produce multiple egg sacs after mating once. Generally, in spiders, earlier egg sacs contain more eggs (Jackson, 1978). In *B. insignis* and *B. longinqua*, perhaps because of the long length of sperm storage and continued food intake, neither sperm nor eggs were limiting, so clutch size did not decrease in consecutive egg sacs. Similarly, clutch size in *Desis marina* (Desidae) does not decrease in consecutive egg sacs (McLay and Hayward, 1987). Copulation duration varied in both species but dramatically so in *B. longinqua*, requiring as little as half a minute to fertilize the eggs, but lasting as long as 4 hours. In *Frontinella pyramitela*, longer copulation results in larger spiderlings in the first egg sac (Suter and Parkhill, 1990), but in *F.pyramitela* and *Phidippus johnsoni*, copulation duration and fecundity are not correlated (Jackson, 1980; Suter and Parkhill, 1990). Reasons why the duration of copulation is highly variable, particularly in *B. longinqua*, are not clear. Various hypotheses, however, have been proposed to account for prolonged copulation (e.g., Suter and Parkhill, 1990); our study tested some of these hypotheses. Mate guarding by males is an unlikely explanation for prolonged copulation in the two species of *Badumna* if first-male sperm priority occurs, but prolonged copulation might function in guarding if sperm mixing or displacement occurs. Studies with spiders generally indicate first-male sperm priority (Austad, 1982; Vollrath, 1980a). The conduit spermathecae of desids such as *Badumna* suggests they have first-male sperm priority (Austad, 1984). Although we do not know if the females of *B. longinqua* and *B. insignis* are polygamous, Costa (1993) hypothesized that resident males of *B. longinqua* guard females from other males; however, this was based on as limited field observations. Mate guarding by females also is unlikely because females can store sperm and because we found no correlation between female fitness and prolonged copulation. All individuals in our study were virgins, so sperm dilution or displacement did not occur. A lack of correlation between the number of palpal insertions and female longevity suggests that males did not contribute longevity-enhancing nutritive substances. We acknowledge, however, that female fitness could have increased but not been detected in the characters that we examined. Fertilization insurance might not operate in *Badumna* because one palpal insertion is sufficient to fertilize all the female's eggs, but it might operate in guarding against displacement or mixing with sperm of subsequent males. The hypothesis that males invest parental care after mating is unlikely because some females are aggressive and attack males after mating. Our results suggest that more palpal insertions by *B. insignis* stimulate oogenesis or oviposition, since more palpal insertions are correlated with a shorter time to the first oviposition. Prolonged copulation, therefore, might be particularly important since female (and male) reproductive success is influenced by how long the female lives; the sooner a female produces eggs, the more clutches it is likely to produce. Longer copulation in this species, however, carries a cost: males that perform more palpal insertions have a greater tendency to be killed by the female. Cannibalism of males by females in *Nephila clavipes* occurs after male persistence in attempting copulation (Vollrath, 1980b). The reasons are unclear why copulation in *B. longinqua* is more prolonged than in *B. insignis*. Although about a quarter of males were attacked, fewer (8.6%) were killed by females of *B. longinqua* than by females of *B. insignis*, of which about one third of the males were attacked and 28.6% killed. Males with more palpal insertions and longer copulation durations were killed more often than those with fewer insertions and shorted copulation durations. Additionally, since relative male weight of *B. longinqua* was correlated with the number of palpal insertions, Future research should examine whether females were less likely to attack or kill males as males approached females in size. *Badumna insignis* and *B. longinqua* share eight of 13 courtship behaviors but differ significantly in certain behavioral aspects. For example, *B. longinqua* exhibits lengthy courtship and copulation, whereas *B. insignis* performs a quick courtship and copulation. In the two species of *Badumna*, courtship probably serves multiple functions. Species recognition probably is facilitated because the two species are morphologically similar and live in close association. Additionally, females of both species are cannibalistic, but males are not attacked until after mating begins, so courtship might suppress female predatory behavior long enough for males to mate. Male assessment of female virginity prior to mating is adaptive in *B. insignis* because males often are killed during mating. Males of *B. insignis* and *B. longinqua* begin courting conspecific females before physically contacting them and do not initiate courtship in heterospecific webs. Females often attempt to kill heterospecifics that enter their webs. Females of the genus *Badumna* might release male-attractant pheromones, as noted in other spiders (Krafft, 1982; Tietjen and Rovner, 1982). Males of *B. insignis* and *B. longinqua* deposit silk in female webs, possibly along with pheromones advertising the male's presence. The weak visual acuity of *B. insignis* (Clemente et al., 2005) suggests that it relies on odor or vibration for conspecific recognition. Lack of any mating attempts between heterospecific individuals, plus attacks by females that frequently resulted in male deaths, suggests that the two species are reproductively isolated by their mating behavior, possibly mediated by species-specific pheromones.

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