

THE MALE MATING SYSTEM IN A DESERT WIDOW SPIDER

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ABSTRACT. Competition among males is a major force shaping sexual selection. We investigated the male mating strategy of the widow spider *Latrodectus revivensis*, a desert species with an annual life cycle. Based on morphology of the sperm storage organs reported for female *Latrodectus*, we predicted that males should guard sub-adult or virgin adult females. In a natural population, we found that males were generally monogamous, cohabiting longer with sub-adult females approaching the final molt than with adult females. Nevertheless, both the duration and timing of male cohabitation were highly variable. Males were found with females from a few days before or after female maturation to over two months after maturation. Maturation of males and females peaked in spring, with a second, smaller peak in summer. Adult males that matured in spring were larger than those maturing later in the summer, while for adult females the pattern was reversed. We suggest that large males of *L. revivensis* that mature in spring maximize reproductive success by mating with virgins. Late males will gain greater reproductive success from mating with large, late-maturing females, but the scarcity of these females in the population at this season may make opportunistic mating with non-virgin females a viable strategy.

Keywords: Mating strategy, *Latrodectus*, sexual cohabitation, size dimorphism

The reproductive success of a male depends on his mating success, i.e., the number of females with whom he mates, and on the number of his sperm that successfully reach and fertilize the females' eggs. In species lacking parental care, where the male's contribution to his offspring is limited to sperm, a male's fitness can increase with additional matings. The combined selection pressures to overcome rival males and convince, force or harass females into mating will shape male behavior, morphology and physiology and affect the mating system (Andersson 1994).

A male's behavior can enhance his reproductive success. In spiders, males may guard females and engage in physical contests with rival males (Elgar 1998). Female receptivity may be reduced after mating by means of male-induced mating plugs (Jackson 1980; Masumoto 1993) and her attractiveness to additional males may be lowered by removing or reducing the female's web and thereby decreasing the surface area of silk with female

pheromone (Watson 1986). Increasing copulation duration (Andrade 1996; Elgar 1995) or the number of copulations (Bukowski & Christenson 1997) and infanticide (Schneider & Lubin 1996) are additional means of assuring male reproductive success in spiders. The male's reproductive success is influenced also by ecological factors such as the availability of females of different developmental stages (adult, sub-adult, juvenile) and reproductive status (virgin or mated), the dispersion of females, male longevity and the operational sex ratio. Thus, phenology, body size, demography and the interactions among males and between males and females can influence the opportunity for males to mate with different partners (e.g., Anava & Lubin 1993; Riechert & Singer 1995). The pattern of sperm use or sperm priority is another factor which can influence male mating success. Sperm priority may be determined in part by the morphology of sperm-storage organs. Austad (1984) suggested that in entelegyne species, which tend to have 'conduit' type spermathecae, first male sperm priority should be the dominant pattern because the first sperm to enter is the first to leave the spermatheca and to fertilize the eggs. Recent evidence, however, suggests

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that both the morphology of sperm storage organs and the pattern of sperm priority is more complex (Uhl & Vollrath 1998; Uhl 2002).

Mating opportunities, ecological factors and the pattern of sperm priority together are expected to influence male mating behavior. Pre-copulatory cohabitation and guarding of sub-adult females is most likely to occur in species with first-male sperm priority and where competition for females is intense, for example where the operational sex ratio is male biased. Post-copulatory cohabitation with adult females could be expected in species where females can mate with more than one male and particularly if there is last-male sperm priority (Eberhard et al. 1993). In cases where sperm priority is not distinct due to sperm mixing, males could cohabit with the females both before and after copulation. Alternatively males could remain with a female only long enough to court and copulate and invest instead in searching for additional females.

A number of studies attempted to correlate the type of spermatheca with mate-guarding behavior. Some comparative studies support the correlation between entelegyne species with 'conduit' type spermathecae and first-male sperm priority, and male cohabitation with sub-adult females (Jackson 1986; Eberhard et al. 1993), and others have shown male preference for sub-adult females in entelegyne spiders (Miller & Miller 1986; Toft 1989; Watson 1990; Fahey & Elgar 1997). In the widow spider, *Latrodectus revivensis* Shulov 1948 (Theridiidae), spermathecae are of the 'conduit' type (Levy & Amitai 1983) and therefore first-male sperm priority is expected. Additionally, the broken embolus of male *Latrodectus revivensis* is likely to act as a mating plug (Berendonck & Greven 2002), which could limit successful sperm transfer by later males. Furthermore, in this species, several adult males may be found simultaneously in the webs of individual females (Anava & Lubin 1993), which provides the potential for male-male competition, and thus, pre-copulatory mate guarding is predicted.

In this study, we conducted observations on a field population over three reproductive seasons and documented demographic changes likely to influence male reproductive success. In addition, we conducted a preliminary test to determine the pattern of sperm priority. Thus, we consider together the influence on

the male mating strategy of two components of intrasexual competition, namely, male competition for females and gamete competition for access to the eggs.

METHODS

Natural history.—The widow spider *L. revivensis* is found in the Negev desert of Israel (Levy & Amitai 1983). The web of *L. revivensis* consists of separate nest and prey-capture components. The nest is a densely woven cone of silk covered externally with plant parts, stones and prey remains and is constructed above ground on shrubs. The capture web includes horizontal non-sticky bridge and platform threads and vertical sticky threads that reach the ground. The diet of *L. revivensis* consists of terrestrial invertebrates: beetles, scorpions, isopods, ants and other spiders (Lubin et al. 1991, 1993).

The spiders have an annual or subannual life cycle. Adults are found throughout the summer and the mating season is from April to September. Females construct egg sacs 2–8 weeks after copulation and hatching occurs one month after egg-laying, from the middle until the end of summer. In a good season, young that hatch early in the summer can mature and complete another reproductive cycle in the same year. Eggs laid at the end of the summer hatch, but the spiderlings over-winter inside the sac and emerge only in spring of the following year. Males are smaller than females and mature faster, with 5–6 molts to adult, compared to 9–10 molts for the females. Once matured, the males leave their nests and enter a female's nest or construct a small silk shelter near the female's nest (Anava & Lubin 1993).

Field observations.—The research was conducted in the northern Negev during the years 1996–1998, in a dry wadi (riverbed) near Sede Boqer (30°52' N, 34°57' E). The vegetation is sparse and composed largely of perennial shrubs (*Zygophyllum dumosum*, *Artemisia herba-alba*, *Reaumuria hirtella*, *Helianthemum* spp., *Hammada scoparia*, *Gymnocarpos decander* and *Noaea mucronata*) on limestone hillsides. The widow spider population was monitored in an area of 25,000 m² during the spring and summer of 1996 (March–September), 1997 (March–June) and 1998 (March–August). To minimize the effect of habitat heterogeneity only spiders found in

the wadi bed and along a strip 500 meters long and 100 wide on the northwest and the southeast slopes were surveyed. Censuses were conducted every 2–4 days in 1996 and daily in 1997 and 1998. In every census the vegetation was searched for nests of juveniles, males and females. Searching for nests biases the census towards females, as nests of males are smaller and less conspicuous, and males leave their nests to search for females. The nests were flagged and the approximate location of each was noted in relation to grid markers placed along the wadi at 10m intervals. Because of differences between the years in season length, population size and phenology, data from the three seasons are analyzed separately.

Pedipalp shape and color were used to distinguish adult males from sub-adults (i.e., individuals one molt before maturation). The presence of a genital opening and the relation between leg length and body size was used to distinguish adult from sub-adult females. To follow and identify the spiders individually, the femur segment of one leg on each side was marked with water-based colors. Every adult and sub-adult male and adult female was marked, measured and released back into its nest. The two size measures taken (± 0.01 mm accuracy) were the length of two segments of the front right leg (tibia+patella) and total body length, from the anterior end of the carapace to the tip of the abdomen. To normalize the data, logarithmic transformations were performed on both leg length and body length. To analyze the change in body size in the population throughout the season, only one measure from each individual was used, taken one day after maturation or on the day the spider was found, if it was already sexually mature when first encountered.

We compared males' survival in their own nests to survival in nests of females, estimated from the field data, based on techniques described in Cox & Oakes (1984). The census data provided the dates of appearance and disappearance of each male. For some individuals the exact date of death (exact failure) was known, while others were right-censored, i.e. the animal survived at least to a particular date, but the exact date of death was not known. In our case, the failure time is within the time interval between two census events. The Kaplan-Meier estimator (Kaplan & Meier

1958), limited to right censored and exact failure data, was used to calculate the survival of males over the two stationary phases in their life, namely, in their own nests and in nests of females. The program SURVIVAL in SYSTAT 7.0 (Wilkinson 1997) was used for the analysis.

We estimated the variation in clutch size and hatching success in the field for comparison with the results from doubly mated females in the lab (see below). Empty egg sacs were collected from deserted nests at the end of seasons 1996, 1997 and 1998. We counted the total number of eggshells to estimate total clutch size and the number of unhatched eggs and dead young. Sacs with signs of predation were not included in the analysis.

Sperm precedence pattern.—To determine sperm precedence pattern we used a double mating technique with sterilized males and fertile (normal) males. There were four treatment groups of sequentially mated females: SS, SN, NS and NN, where S represents sterilized males and N represents untreated (normal) males. The females in the NN treatment were introduced to a sequence of two fertile males and the females in the SS treatment were introduced to a sequence of two sterile males. In the SN group the first male introduced to each female was sterile and the second fertile and in the NS group the first male introduced to each female was fertile and the second sterile. Males were virgins in all cases and females were virgins at the start of the experiment. The experiment was conducted at c. 24°C and under artificial light adjusted to the ambient light regime. Some of the spiders were reared in the laboratory from hatching to maturation and some were collected in the field 2–3 molts prior to maturation. The spiders were fed with live prey (fruit flies, crickets, grasshoppers and beetles). Each individual was kept in a separate container.

The experiment included 30 males and 15 females. A week to 10 days after the last molt the males of the S group were exposed to 8.3 min. of 600 RAD/min. of Cobalt 60 (a total dosage of 5000 RAD). This amount of radiation is deemed sufficient to damage the DNA of the sperm cells without appreciably affecting their mobility (Jackson 1980; Vollrath 1980; Austad 1982; Kaster & Jakob 1997). The males and their female partners and each pair's mating sequence were chosen randomly.

Table 1.—Total clutch size and proportion of eggs hatched (median and range) in egg sacs collected from nests in the field during 1996, 1997 and 1998. Data are shown only for the first four eggsacs. Sacs with evidence of predation were not included.

Year	Eggsac 1	Eggsac 2	Eggsac 3	Eggsac 4
A. Clutch size				
1996	263 (18–390)	183 (21–513)	130 (53–623)	167 (6–203)
1997	359 (0–493)	304 (190–377)	208 (134–327)	322 (171–354)
1998	316 (18–632)	274 (40–513)	282 (53–623)	186 (140–233)
B. Hatching success				
1996	0.99 (0.25–1)	1 (0.15–1)	1 (0.89–1)	1 (0.99–1)
1997	1 (0–1)	1 (0.99–1)	1 (0.99–1)	0.99 (0.95–1)
1998	0.99 (0.2–1)	1 (0.84–1)	0.99 (0.89–1)	1 (1)
C. Sample size (Number of eggsacs)				
1996	6	11	9	4
1997	9	5	4	3
1998	16	10	6	2

The first male was left in the female's container for 5 h after which he was removed and a second male was introduced for another consecutive 5 h. In *L. revivensis* it was difficult to determine whether copulation had occurred due to the small size of the male and the color resemblance of male pedipalps and female abdomen and genital opening. Preliminary observations suggested that 5 h was sufficient to allow successful copulation. In nature, mating occurs during the day, as at night females hunt actively on their webs. Therefore, we conducted the mating experiments in the lab during the day. Males and females were measured before the experiment and each male was used only once.

The egg sacs produced by each female were numbered, and the dates of construction and hatching were recorded. The first four egg sacs of each female were opened two months after they were built, a sufficient time for all the fertile eggs to hatch. Using a dissecting microscope and a counter, we recorded for each egg sac: total number of eggs, number of spiderlings, number of eggshells and the number of unhatched eggs. Usually the number of eggshells closely matched the number of spiderlings. We used the data to determine the proportion of eggs that hatched in each treatment. Because of small sample sizes and high variability in proportion of eggs hatched between females and between different egg sacs of a single female, we have not attempted to calculate P2 values (proportion of eggs fer-

tilized by the second male to mate, Andrade 1996; Schneider & Lubin 1996), but rather we report the results as the proportion of eggs hatched and total clutch size for the first four egg sacs for all 15 females (Table 1).

RESULTS

Maturation time and survival.—Males began to mature before females (Fig. 1). The greatest number of adult males was found when half of the females in the population were still sub-adult. The number of adult females peaked between the end of April and the beginning of May, by which time the number of adult males was declining.

In 1996, only one dead male was recovered and therefore survival time could not be calculated. Fifty-two males were found, 18 in their own nests and 33 with were first found with females. Three of the 18 males (16.7 %) that were found as adults in their own nests were later discovered cohabiting with females. One of the three males moved at least 8 m to the female's nest. Two males cohabited with two different females, moving at least 10 and 80 m, respectively, between successive females.

In 1997 we compared the survival of marked males when in their own nests with their survival once they reached the nest of a female. Of 81 adult males that were captured, marked and released, 36 (44.4%) were found initially in their own nests and 45 were encountered for the first time in a female's nest.

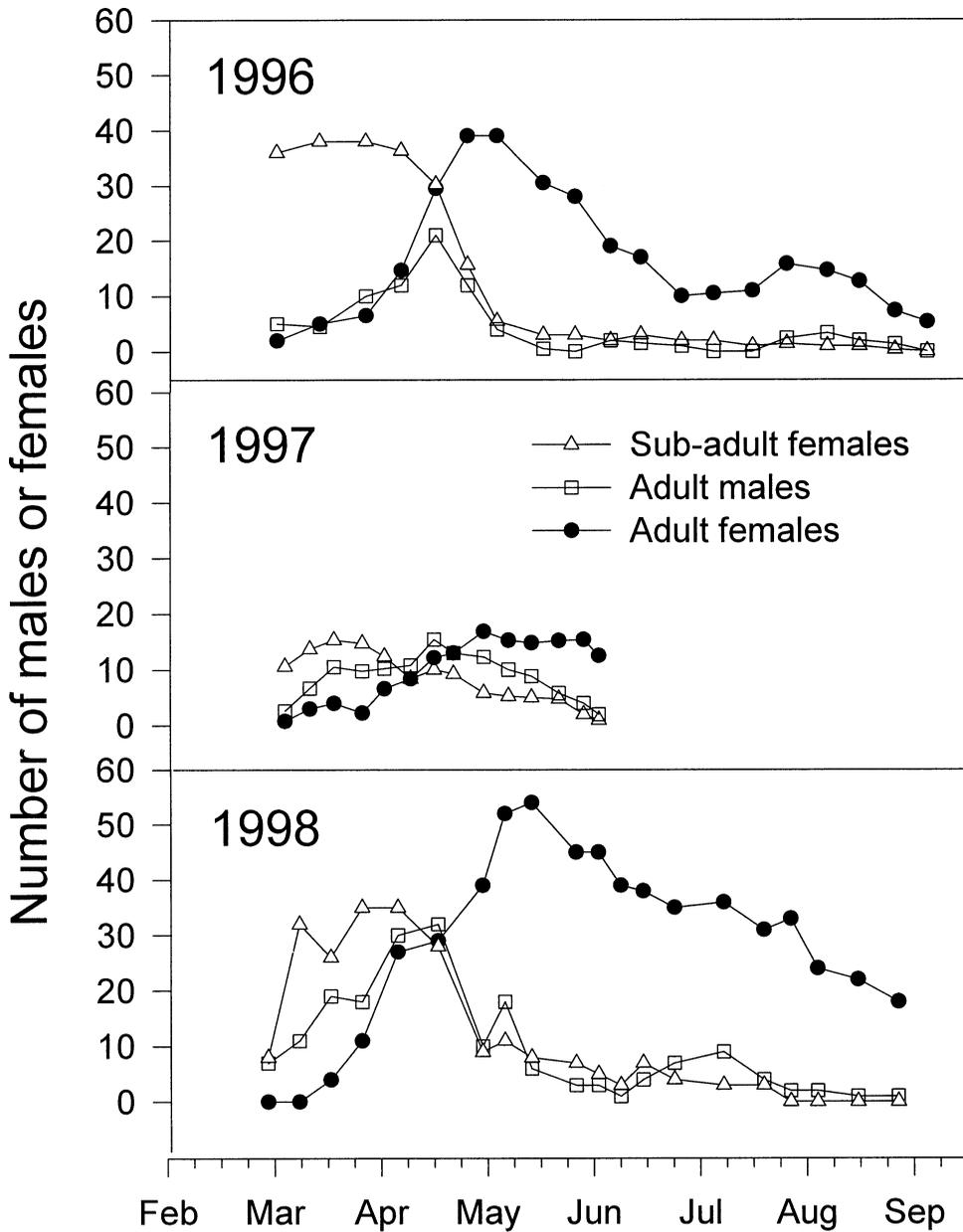


Figure 1.—Number of adult females, sub-adult females and adult males averaged over 7–10 day intervals in 1996, 1997 and 1998.

Only three males (5.6%, $n = 36$) encountered first in their own nest, were later found cohabiting with a female. These males moved a minimum of 3, 4 and 12 meters between their own nests and those of the females. Of the males seen cohabiting with females, 13% were found dead and apparently sucked dry in the females' nests. These males were most

likely cannibalized by the females. Males survived significantly longer in their own nests than when cohabiting with females (Kaplan-Meier estimation 12 days vs. 9.4 days, respectively, $\chi^2 = 8.74$, d.f. = 1, $P = 0.003$).

In 1998, 103 males were marked, 52 (50.5%) of which were found initially in their own webs and the rest in webs of females.

Three of the males marked in their own webs (5.8%) were later found with females. Males survived 33.9 days in their own nests and 28.9 in nests of females (Kaplan-Meier estimation, $\chi^2 = 0.21$, d.f. = 1, $P > 0.05$).

Timing and duration of cohabitation.—

In 1996, most males were found with females around the time when the females molted to adult (Fig. 2). Nevertheless, males were also found cohabiting with females up to 70 days after female maturation. In 1997, most males were found cohabiting with females just before they matured to about a week after they molted to maturity, and some males were found with females 50–60 days following female maturation. In 1998 males were found with females up to 85 days after female maturation, especially late in the season.

In all three seasons, males tended to stay longer in nests of sub-adult females than in those of adult females (Fig. 3). The difference was significant in 1996 (Mann-Whitney $U_{10,27} = 215$, $P = 0.03$), but not in 1997 ($U_{11,42} = 270$, $P = 0.308$) or in 1998 ($U_{13,66} = 464$, $P = 0.64$). These results include cases where a male stayed in the nest even after the female had left the nest. When these cases were removed there was still a significant difference in 1996 ($P = 0.04$). The maximum time a male remained in a female's nest was 29, 35 and 42 days during 1996, 1997 and 1998, respectively.

Male and female size.—There were significant differences between the years in the body sizes of males and females (ANOVA, $P < 0.001$) and therefore, body size trends were analyzed separately for each year.

To determine if the size of females and males that matured early or late in the season differed, we regressed the means of body and leg length of individuals measured over a period of 7–10 days against the median date of that period. Median dates were used because the date of measurement was frequently not the exact date of maturation (see Methods). In all three years, males that matured later in the season were smaller than males that matured at the start of the season (Fig. 4). The decline in total length was significant in 1996 ($r = -0.865$, $P = 0.001$, $n = 11$) and in 1998 ($r = -0.56$, $P = 0.02$, $n = 18$), but not in 1997 ($r = -0.457$, $P = 0.185$, $n = 10$). Male leg length showed a similar decline in 1996 ($r = -0.813$, $P = 0.002$, $n = 11$) and 1998 ($r =$

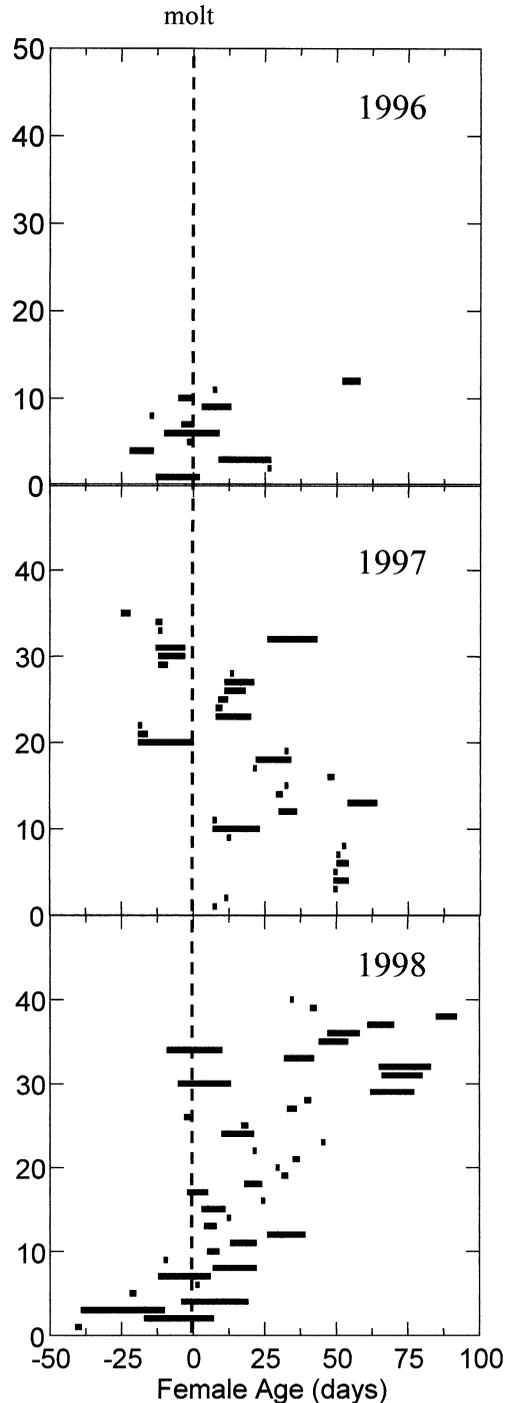


Figure 2.—Timing and duration of male cohabitation with females in 1996 ($n = 12$ males), 1997 ($n = 35$ males), and 1998 ($n = 40$ males). Individual males are arranged along the Y axis in order of their appearance from the beginning of the season to the end of the season. Female age is relative to the day of the molt to adult (day = 0).

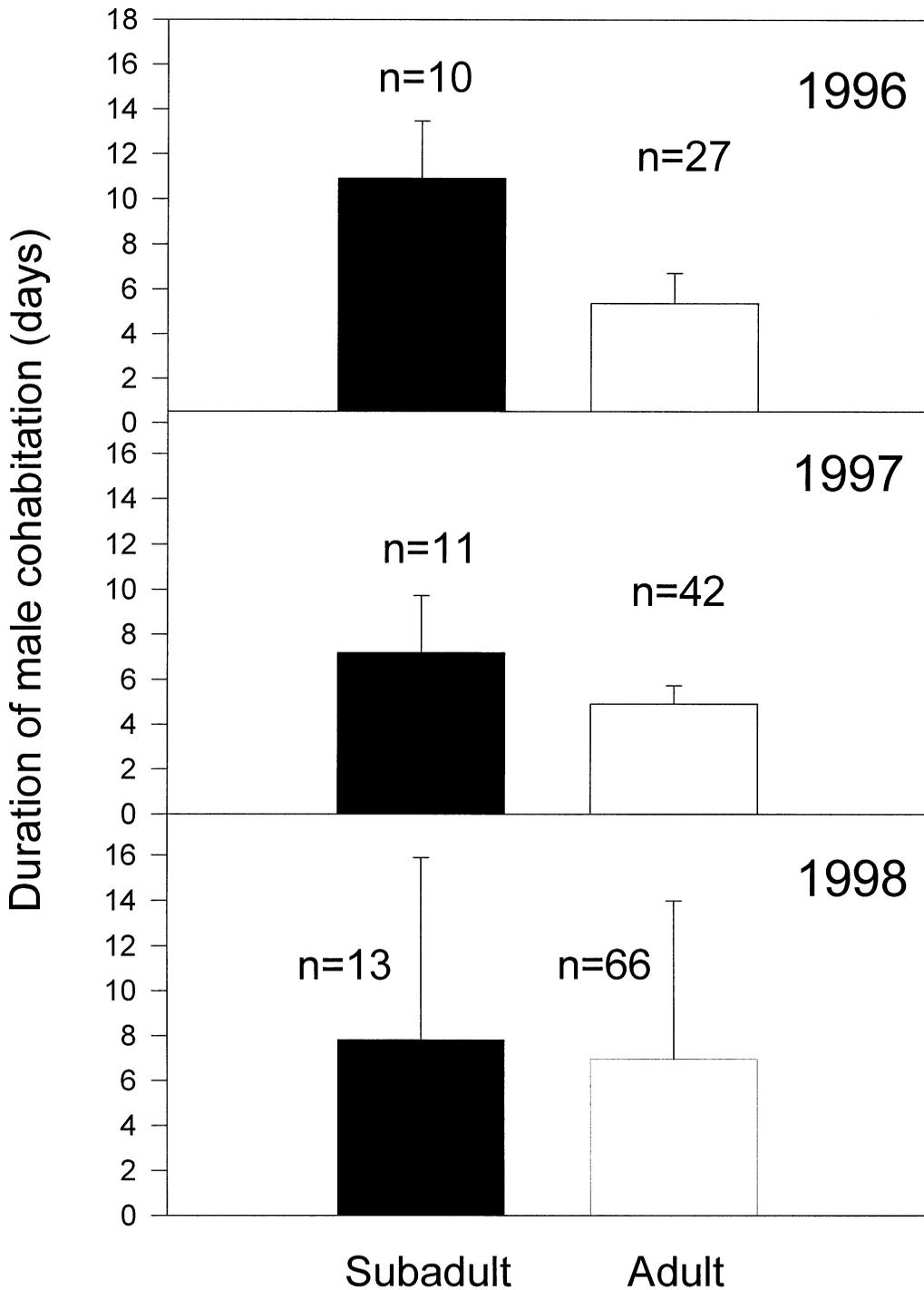


Figure 3.—Cohabitation duration in days (mean, s.d.) of adult males in nests of sub-adult and adult females in 1996, 1997 and 1998. Sample sizes are shown above the bars.

-0.52 , $P = 0.03$, $n = 18$), but not in 1997 ($r = 0.09$, $n = 10$). The change in leg lengths in 1997 was best described by a first order polynomial ($P = 0.046$, $n = 10$), showing a decrease in length from March until May.

Female size showed a trend opposite to the male size trend: both body and leg length tended to increase over the season (Fig. 4). For body length the increase was significant in 1996 ($r = -0.819$, $P = 0.013$, $n = 8$), but not in 1997 ($r = 0.508$, $P = 0.245$, $n = 7$) or in 1998 ($r = 0.329$, $P = 0.2$, $n = 16$). Leg length increased significantly in 1996 ($r = 0.819$, $P = 0.013$, $n = 8$) and in 1997 ($r = 0.793$, $P = 0.033$, $n = 7$), but not in 1998 ($r = 0.163$, $P = 0.55$, $n = 16$).

The body sizes of adult females and males found together in a nest were not correlated (Spearman rank correlation, $r_s = 0.239$, $n = 27$, $P > 0.1$; $r_s = 0.09$, $n = 35$, $P > 0.1$; $r_s = 0.024$, $n = 61$, $P > 0.1$ in 1996, 1997 and 1998 respectively). Nor was there a significant correlation between pairs of males and females for leg length or body condition index (body length/leg length) ($P > 0.1$ in all years).

A difference in size between adult males in their own webs and males found cohabiting with females could indicate female mate choice or male-male competition for females. However, when time in the season was accounted for by analysis of covariance (ANCOVA), there was no significant difference in leg length or body length of solitary and cohabiting males in 1996 (leg length: $F_{1,50} = 0.379$, $P = 0.541$; body length: $F_{1,50} = 1.028$, $P = 0.316$) or in 1997 (leg length, $F_{1,80} = 0.804$, $P = 0.373$; body length, $F_{1,80} = 0.13$, $P = 0.719$).

Mating system.—In all three years, most males visited only a single female (Fig. 5). In 1997, there were no males observed in more than a single female nest; in both 1996 and 1998, 4% of males were found in nests of two females. A greater proportion of females, however, were visited by more than a single male (Fig. 6). Five percent of females were visited by more than a single male in 1996, 28% in 1997 and 15% in 1998.

Sperm precedence.—In the field data, we found large variation in clutch size in all three seasons. The median proportion of eggs that hatched was near 1, but with considerable individual variation (Table 1).

The median proportion of eggs hatched in

the NN treatment was between 0.5 and 0.845. Eggs laid by the females mated with two sterile males (SS treatment) did not hatch at all. In both the SN and NS treatments, two females each produced 2–4 successive eggsacs with no fertile eggs, while in the other two females in each treatment, hatching proportions were variable (SN: 0.37–0.99, NS: 0.23–0.99). The clutch size of the four females that produced no fertile eggs was within the range of clutch sizes of females that did produce hatching young and of females mated to two fertile males (Table 2).

There was no significant difference in clutch size between sacs 1–4 within each treatment (Table 2, ANOVA: $F_{3,45} = 0.401$, $P > 0.05$), nor was there a difference between the four treatments (ANOVA: $F_{3,45} = 2.698$, $P > 0.05$). The proportion of eggs that hatched in successive sacs within each of the three treatments did not increase or decrease significantly (NN: $r_s = -0.370$, $n = 16$; SN: $r_s = 0.043$, $n = 15$; NS: $r_s = 0.019$, $n = 14$; Table 2) although a negative trend was seen in the NN group. We found no significant difference between the treatments in the interval between mating and egg-laying (Kruskal-Wallis, $P = 0.833$, d.f. = 3, $n = 15$) and only a small fraction of the variability in hatching proportion was explained by the interval between mating and oviposition ($R^2 = 0.045$, $P = 0.450$, $n = 15$).

DISCUSSION

Both males and females had two peaks of maturation, a larger one in spring and a small one in summer. Adults are strongly sexually dimorphic in body size and the difference in size increased as the season progressed. Thus, males that matured early in the season were relatively large, while females were small; males maturing late in the summer were small, while late-maturing females were large. Males matured before females and either remained in their own nests or joined sub-adult females in their nests. Males tended to stay longer with sub-adult females close to the time of the molt to sexual maturation than with adult females. Nevertheless there was considerable variation in the timing and duration of male cohabitation in relation to female maturation date. Adult males were seen cohabiting with sub-adult or adult females a month before and more than two months post

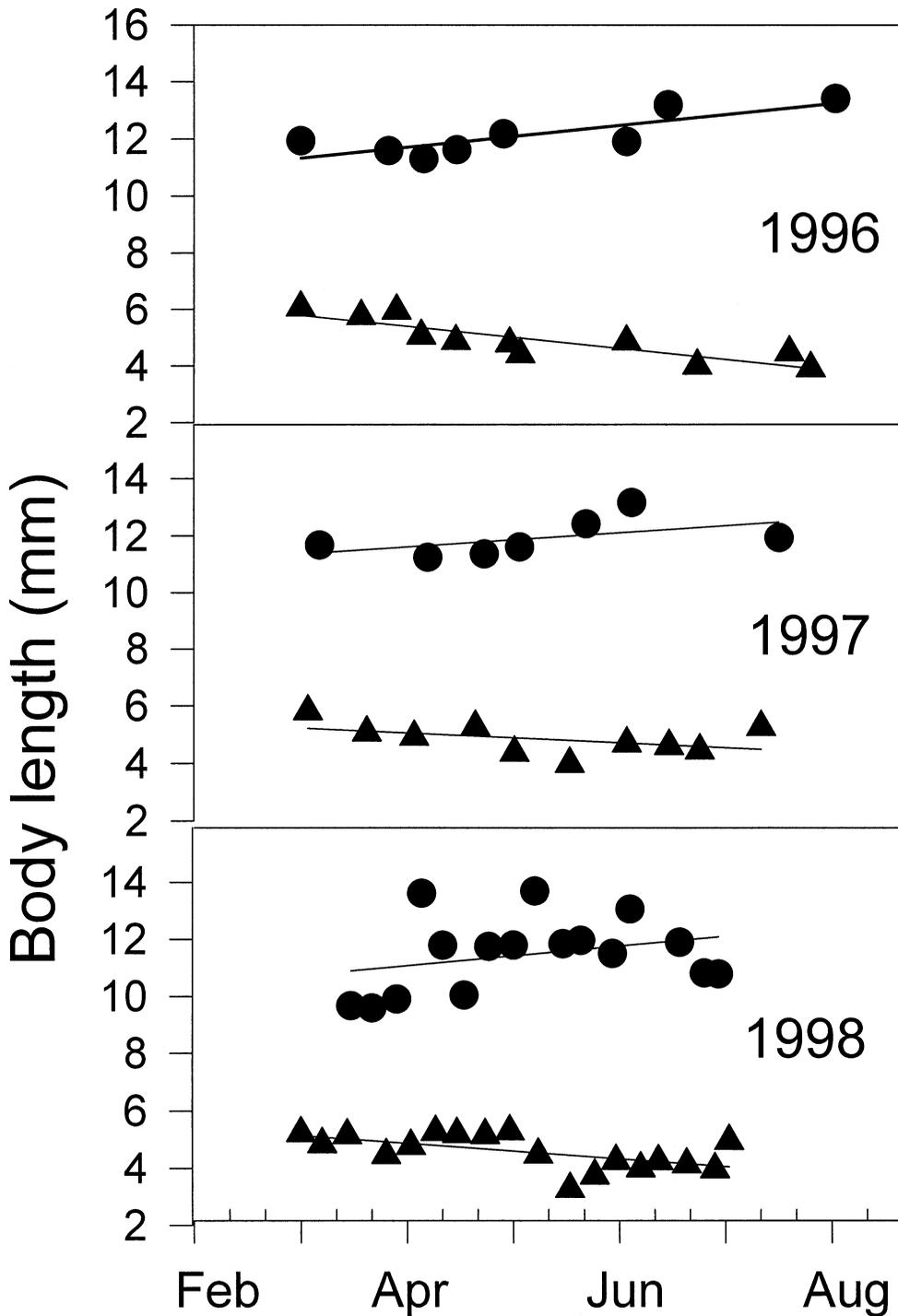


Figure 4.—Body sizes (total length, mm) of adult females (●) and males (▲) throughout the season. Regressions are of 10-day (1996) or 7-day (1997 and 1998) averages (see text). Each individual measurement was used in the regression only once, at the date the spider matured or was first encountered as an adult. There were 80 males and 33 females in 1996, 59 males and 79 females in 1997 and 103 males and 66 females in 1998.

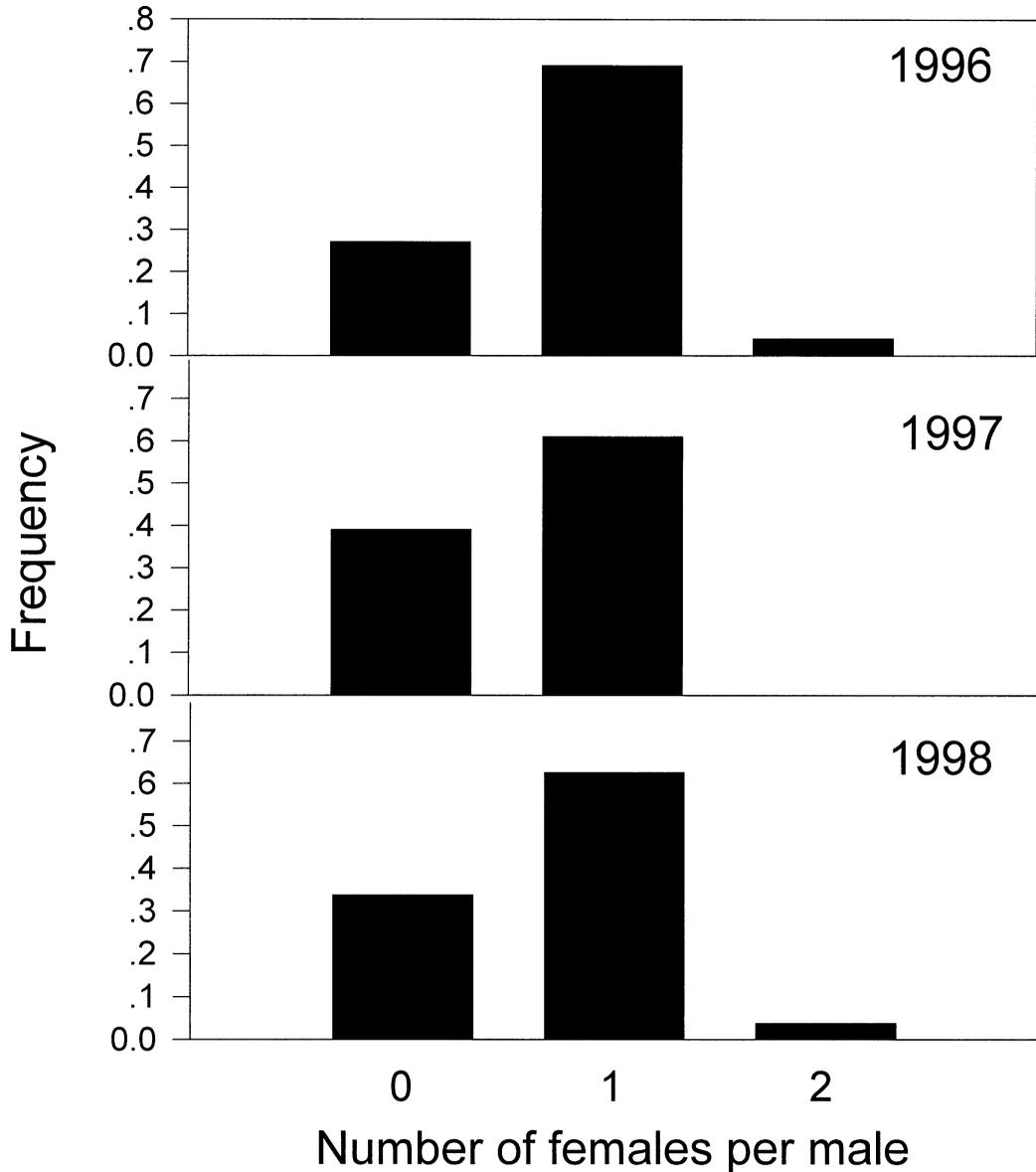


Figure 5.—Frequency distribution of the number of females that were visited by males during 1996, 1997 and 1998. Sample sizes were 81 adult females in 1996; 25 females in 1997; 99 females in 1998.

maturation, and for periods of a day to more than one month. The field data indicate that most of the males in the population were monogamous, but that females were often exposed to visits of several males.

Male monogamy.—Male monogamy is expected when the probability of encountering and mating with additional females is low (Andersson 1994; Riechert & Singer 1995). This would be the case if non-virgin females

resist additional matings (Reynolds 1996), if male mortality risks during searching or on the female's web are very high (Vollrath 1980; Vollrath & Parker 1992; Andrade 1996) or if there are morphological or physiological constraints on multiple mating in males (e.g., loss of a pedipalp during mating; Knoflach & van Harten 2001).

In *L. revivensis* females in the laboratory, resistance to additional copulations appeared

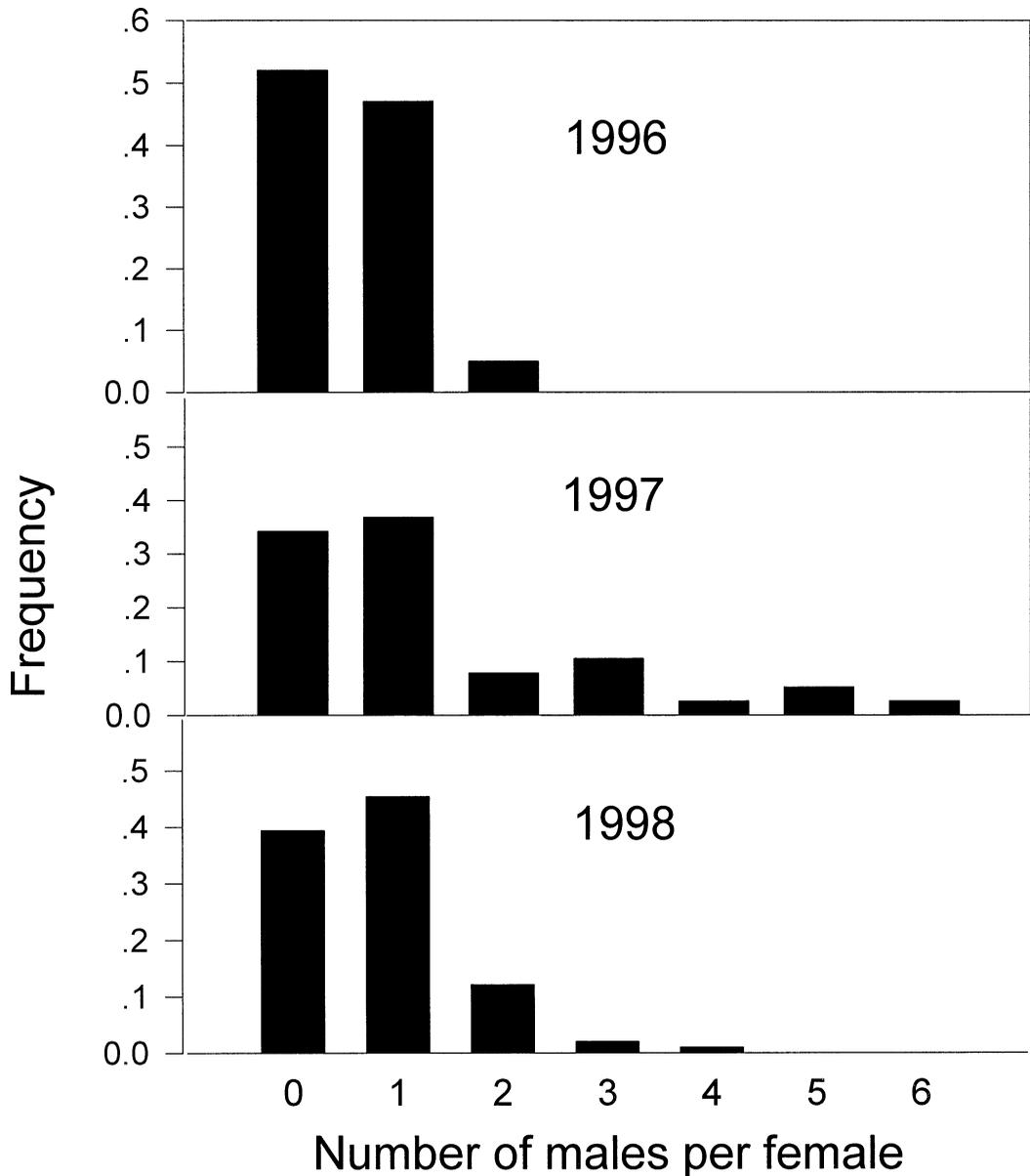


Figure 6.—The number of males that visited females' nests during 1996, 1997 and 1998. Sample sizes were 53 males in 1996; 53 males in 1997; 58 males in 1998.

to increase with time from the first mating (pers. obs). In the field, however, we found males with females that were several weeks after their final molt, and even with females with eggsacs. Thus, mating opportunities do not seem to be restricted to virgin females. Mortality on the female's web due to female cannibalism was not high (13%) by comparison with some other widow species (e.g. 65%

in *L. hasselti*, Andrade 1996). Thus, terminal investment of the male in a single female, as occurs in *L. hasselti*, is not expected and does not explain monogamy in *L. revivensis*.

Mortality of males in their own nests was relatively low (3–6%), but very few males that were marked in their own nests were found later in webs of females in the study area (<4%), suggesting that mortality during

Table 2.—The proportion of eggs that hatched and total clutch size of four eggsacs produced sequentially. The data were collected from 46 eggsacs produced by 11 females.

Female	Treatment	Proportion hatched (clutch size)			
		Eggsac 1	Eggsac 2	Eggsac 3	Eggsac 4
1	NN	0.81 (137)	0.85 (141)	0.91 (126)	0 (46)
2	NN	0.45 (214)	0.58 (156)	0.62 (122)	0.5 (90)
3	NN	0.88 (179)	0.91 (123)	0 (190)	0.70 (187)
4	NN	0.97 (102)	0.81 (167)	0.78 (94)	—
5	SN	0.92 (167)	0.65 (180)	0.99 (145)	0.96 (142)
6	SN	0.55 (163)	0.80 (128)	0.37 (176)	0.67 (101)
7	SN	0 (151)	0 (99)	0 (176)	0 (100)
8	SN	0 (104)	0 (77)	0 (98)	0 (69)
9	NS	0.99 (192)	0.23 (119)	0.85 (141)	—
10	NS	0.35 (139)	0.98 (292)	0.97 (234)	0.91 (160)
11	NS	0 (169)	0 (177)	0 (144)	0 (110)
12	NS	0 (223)	0 (156)	—	—
13	SS	0 (146)	—	—	—
14	SS	0 (244)	0 (285)	0 (203)	0 (209)

searching for females could be high. In juvenile and sub-adult females, 40% of spiders on average were estimated to have died during the movement phase of web relocation (Lubin et al. 1993). Alternatively, marked males may have moved out of the study area to find females elsewhere, while the unmarked males that appeared in nests of females were likely immigrants from outside the census area. The large distances moved by marked males (up to 80 m) support this idea. Furthermore, if males are attracted directly to webs of recently molted females by means of volatile pheromones in the female web silk (Schulz & Toft 1993; Miyashita & Hayashi 1996; Papke et al. 2001), then the high mortality typical of random mate search would be eliminated or reduced. Thus, it is possible that male monogamy is not due to costs of mating dispersal in this species.

Levi (1959) observed that male *Latrodectus* often lost the tip of the embolus, and emboli could be found inside the spermathecae of females, suggesting that the embolus may act as a mating plug. This idea has received support from a recent morphological study (Beren-donck & Greven 2002). If males who have lost an embolus tip are unable to re-charge the palp, or are unable to deliver sperm to the spermatheca, then a male could successfully copulate only twice. Thus, if a male copulated twice with the same female, he would be effectively monogamous. This explanation for

finding marked males in the field with at most two females remains to be tested.

Cohabitation.—Based on spermathecal structure, we predicted that *L. revivensis* should have first-male sperm priority and that males should attempt to mate with virgin females (Austad 1984). As a corollary, we predicted mate guarding of sub-adult females nearing maturation. Some cohabitation with sub-adults occurred in our field population, but most cohabitation occurred just after the female's molt to maturity. Preliminary data show that males are not attracted to silk from webs of sub-adult females, and that this silk lacks some volatile compounds present in webs of recently molted adult females (Lubin & Papke unpubl. data). Furthermore, sub-adult females often shifted to a new website within a few days of a male arriving at the nest (Lubin et al. 1993), which suggests that sub-adult females are not always tolerant of the male's presence. Thus, a strategy of searching for and guarding sub-adult females until they molt may be less rewarding than seeking adult virgin females. Recently molted females attract males from several meters away (unpub. obs.). Another apparently anomalous behavior is explained in this context: we found that after molting to maturity, males often remained in their own nests for very long periods; up to 42 days. They do not feed during this time and thus should lose both body mass and potential mating oppor-

tunities. The behavior can be understood, however, if males remain in their nests until the pheromone of a female is detected, and then move rapidly towards the source. Such a movement strategy would also minimize the risk of mortality associated with random searching. To our knowledge, this prolonged delay between maturation and leaving to search for females has not been noted in other studies.

Sperm precedence.—The pattern of hatching success in the double-mating experiment would suggest sperm mixing. However, problems emerged with the sterile male technique of assessing sperm priority, and consequently we are unable to define the pattern of precedence. First, as we did not observe the pairs continuously during the 5 hours that each male was left with a female, we could not be sure that copulation had indeed occurred. Second, even if the male copulated, he may not have transferred sperm. Bukowski & Christenson (1997) examined sperm remaining in male pedipalps and showed that sperm transfer does not always take place in spiders even when the pair copulate. If male *L. revivensis* consistently break off the terminal sclerite of the embolus during copulation (Levi 1959; Berendonck & Greven, 2002), it may be possible to determine if a male copulated successfully by examining the male palps after mating for the loss of an embolus tip or, alternatively, by counting sperm in the pedipalps (Bukowski & Christenson 1997; Schneider et al. 2001). Finally, a male may copulate with one or both palps, filling one or both of the female's spermathecae. If the broken embolus tip acts as a partial or complete barrier to further sperm transfer, then we should expect a strong first male priority effect as a consequence of pre-copulatory 'sperm' competition. In the SN treatment in our experiments, two females produced a succession of completely infertile clutches. This could be explained by the presence of embolus tips of the sterile (first) male, which blocked both spermathecae, and thus not allowing the fertile (second) male to inseminate the female. However, similar failures occurred in two females in the NS treatment, an observation which is difficult to explain. Clearly, further experiments remain to be done to investigate the relationship between mating sequence and sperm priority.

Male mating strategy.—Several features which may be under direct or indirect sexual selection are evident in the male mating strategy of *L. revivensis*. These include: protandry, male body size, searching and cohabitation with adult and sub-adult females. Protandry, or early maturation of males, is common in spiders and other arthropods, and is often thought to increase chances of obtaining females, particularly under scramble competition (mate opportunity hypothesis; Morbey & Ydenberg 2001). If a broken embolus indeed acts as a mating plug and female re-mating is limited, then protandry in this species may be selectively advantageous to males.

Linked to protandry is the large sexual size dimorphism and seasonal variation in male body size. Males mature at an earlier instar than females, while selection on fecundity presumably favors large body size and hence later maturation in females (Lubin et al. 1993). However, the relative timing of maturation, and the resulting body sizes, differ for individuals that mature in spring and those maturing later in the summer. Males that mature in spring have had 6–8 months to grow, assuming they hatched in the autumn, while summer maturing males are from eggs that hatch in spring and have only 3–4 months of growth from hatching to maturation. Thus, spring maturing males are large and in good body condition and summer maturing males are small. Spring maturing females, however, are small relative to summer maturing ones, as food supplies, particularly of large arthropods that constitute the main prey of females (Lubin et al. 1993), are more abundant in the summer months. These observations suggest that there are different selective forces acting on maturation time and body size in males and females. In males, sexual selection promotes early maturation for both development peaks (spring and summer). For spring females, early maturation is also advantageous, because their young will hatch in spring or early summer when insects are most abundant. Thus, spring maturing females are relatively small, while summer females (that produce overwintering young) are not constrained by timing of maturation and fecundity selection will be manifested in larger body size.

The above decisions relating to the timing of maturation and their effects on body size of males and females, have further conse-

quences for male behavior. In spring there are many virgin females and males can adopt one of two search strategies: high-risk random search and cohabitation with sub-adults or low-risk directional movement to webs of newly-molted virgins, where they face competition from other males (Anava & Lubin 1993). Large body size is likely advantageous in male-male competition (Elgar 1998). As the reproductive season progresses, virgin females are sparsely distributed in time and space. Male search strategy may shift to attempting to mate with non-virgin females when the chance of finding a virgin female is low. Observations of males in nests of females that were many weeks post-maturation support this idea. We have also observed males attempting to copulate opportunistically with a female that already had egg sacs and was engaged in feeding on large prey. Whether mating with older females is a distinct male mating 'strategy' or a case of late-maturing males making 'the best of a bad job' is not clear. Nevertheless, late males have one advantage in that late females are large and have high fecundity and thus may have greater reproductive success than early males. In summary, the male mating strategy appears to be a flexible outcome of the interaction between seasonal growth decisions, availability of potential mates and possible morphological constraints.

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