



ARTICLES

Vibratory courtship in a web-building spider: signalling quality or stimulating the female?

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Courtship behaviour in spiders in the form of premating vibrations by males may function (1) as a male identity signal used for species recognition, (2) in suppression of female aggressiveness, (3) to stimulate female mating behaviour, or (4) as a quality signal used in female choice. We investigated the function of web vibration by male *Stegodyphus lineatus* in a series of experiments. Regardless of vibratory performance, all males mated successfully with virgin females but only 56.4% of males mated with nonvirgin females. Vibratory performance did not influence male mating success, but heavier males had a higher probability of mating with mated females. Males vibrated less often and produced fewer vibrations when introduced on the web of a mated female. Males that vibrated webs of virgin females mated faster than nonvibrating males, but there was no effect of vibration rate or body mass. There was no effect of male vibratory effort or vibration rate on female reproductive success measured as time to egg laying, clutch size, number of hatched young, number of dispersed young and offspring body mass after a single mating. Males vibrated on abandoned virgin female webs but the response decreased with increasing duration of female absence, suggesting that females produce a web-borne pheromone, which elicits male vibrating behaviour. Mated females were less receptive and not stimulated by male vibrating behaviour. We conclude that male premating vibrations in *S. lineatus* do not function as a male quality signal selected via female choice. Rather, the primary function of this behaviour may be to stimulate a receptive female to mate.

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The function of courtship behaviour in spiders has traditionally been interpreted as species recognition, sexual arousal or inhibition of female predatory tendencies (Montgomery 1903, 1910; Bristowe & Locket 1926; Crane 1949; reviewed in Robinson & Robinson 1980; Jackson 1982). The necessity to inhibit female predatory tendencies results from the cannibalistic nature of spiders in general and from sexual cannibalism in some species in particular (Darwin 1871; reviewed in Elgar & Crespi 1992). Alternatively, vibratory courtship in spiders through signalling (Kotiaho et al. 1996; Parri et al. 1997; Singer et al. 2000) could provide females with information about male quality (Trivers 1972; Zahavi 1975). Sexually selected signals can be reliable indicators of male quality if their reliability is maintained by a cost of production (Zahavi 1975; Grafen 1990). Thus, female

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wolf spiders *Hygrolycosa rubrofasciata* choose mates on the basis of male drumming activity, which is correlated with viability (Kotiaho et al. 1996). Courtship drumming is also condition dependent and energetically costly, further supporting the quality-signalling hypothesis (Kotiaho 2000).

We investigated the function of vibratory courtship behaviour in the web-building spider *Stegodyphus lineatus* (Eresidae), in which courting males often vibrate the female's web before mating (Erez 1998). We considered four hypotheses that are not mutually exclusive: (1) prevention of interspecific mating; (2) reduction of female predatory tendency; (3) arousal to a state of copulatory readiness; and (4) quality signalling (Table 1).

Species-specific or sex-specific signalling (hypotheses 1 and 2) implies that premating vibration is used as a recognition signal. These hypotheses predict that premating vibration should be necessary for mating to occur and that vibrations should be stereotypic to allow recognition of conspecific males as mating partners (Robinson &

Table 1. Functional explanations for vibratory courtship

Hypotheses	Predictions
Prevention of interspecific mating	No mating without vibration
Reduction of female predatory tendency	No mating without vibration
Sexual arousal	Vibration reduces latency to mating
Quality signalling	Vibration rate increases male mating success, correlates with female fitness, and is condition dependent

Robinson 1980). Failure to provide the appropriate signal would result in rejection or injury for a given male.

The 'sexual arousal' hypothesis predicts that vibrations will increase the readiness of a female to mate, reducing the time from female encounter until copulation. For copulations in *S. lineatus* to take place, the female raises her prosoma to allow the male to position himself underneath and insert his pedipalps into the genital openings. This position seems to be crucial for successful copulation and no mating was observed otherwise (personal observations from the laboratory and the field). Females inhabit narrow nests and copulations take place in the wider entrance or outside the nest where the male can reach the female's genital openings. Females usually sit deep inside the nest, which prevents the male from copulating immediately. If the female does not move out of the nest on the male's first approach to the entrance, the male returns to the web, vibrates and re-enters the nest repeatedly, until the female moves out and into the mating position. Premating vibration may function as a cue that stimulates the female to move into this position.

Finally, the 'quality-signalling' hypothesis predicts that females will choose males on the basis of their vibratory performance, and that male vibratory performance will correlate positively with female fitness. Female spiders may use a bet-hedging strategy by indiscriminate acceptance of the first male to ensure fertilization of their eggs, and then accept additional males on the basis of their courtship performance. If male spiders can distinguish between virgin and mated females and adjust their courtship behaviour accordingly, we predict they would increase vibratory performance when courting a mated female. Alternatively, females may preferentially use sperm from the best performing male (cryptic female choice). In that case, males should do their best on every encounter, and no difference is expected between the courtships of virgin and mated females. Because the quality-signalling hypothesis also predicts that vibrations should be condition dependent (Kotiaho 2000), we tested the effect of male body condition on vibratory performance.

Both quality-signalling and sexual arousal hypotheses predict that male vibratory performance should increase the propensity of females to mate. However, there is an important distinction. The sexual arousal hypothesis suggests that male vibratory performance will reduce the time to copulation by synchronizing male and female precopulatory behaviour, but should not affect the female's ultimate decision on whether to accept a particular male as a mate. Thus, behavioural or morphological

factors other than vibratory courtship such as male body mass can affect male mating success (Singer & Riechert 1995). In contrast, the quality-signalling hypothesis predicts that vibratory performance will affect either female acceptance of a particular male as a mate or postcopulatory female choice. In particular, vibration rate may be a good predictor of female choice (Kotiaho 2000).

In our experiments, we observed male vibratory behaviour and female reaction during mating with virgin and mated females. We examined the effect of male vibratory performance on female fitness-related parameters such as clutch size, hatching success, survival of young until the dispersal stage and body mass of the dispersing spiderlings, while taking into account the possible effects of male condition and male body mass. We also investigated whether male vibratory behaviour is triggered by female web-borne cues, which may change with the reproductive state (virgin or mated) of the female.

METHODS

Study Species

Stegodyphus lineatus Latreille 1817 (Eresidae) is a web-building spider that is found in arid and semiarid habitats around the Mediterranean basin. The spiders are common but patchily distributed. Females are extremely sedentary and build solid conical nests with large capture webs. Males leave their nests after the final moult and wander in search of females. The mating season begins in March and lasts until June (Schneider & Lubin 1996, 1997). Males may stay in the female's nest for 1–18 days after mating, and females may encounter multiple males during the mating season (Schneider 1997). Females are semelparous and provide extended maternal care for the offspring, which consume the mother about 2 weeks after hatching (Schneider 1992). Females may be aggressive towards males, and occasionally injure or kill them (Schneider & Lubin 1997; Erez 1998; personal observations), but we have never observed cannibalism during courtship and mating.

We collected 250 subadult *S. lineatus* in their natural habitats in Israel in March 2000 and brought them to the Sede Boqer Campus of Ben Gurion University. Spiders were kept individually in plastic containers (5 cm diameter × 10 cm high) with mesh lids and reared to maturity on a diet of desert locusts, *Locusta migratoria*, crickets, *Acheta domestica*, and flour beetles, *Tenebrio molitor*. We kept the spiders outdoors under natural temperature and light conditions protected partially against

direct sun by shade cloth. After the final moult the adult spiders were measured and weighed. We used prosoma width as a measure of male body size, following Schneider & Lubin (1997). See Schneider (1997) for details of the measuring procedure. Adult spiders and hatched young were released back into their natural habitat after the experiments.

Mating with Virgin and Mated Females

We randomly paired 78 virgin males and females and obtained data on vibratory courtship from 75 matings. We introduced a male on to the female's web by inducing him to run on to a wooden stick close to the web. When the male encountered the web he left the stick and moved on to the web. We observed the behaviour of the pair for 3 h or until copulation occurred and determined the duration of the first copulation for 33 mating pairs. Males usually initiated courtship behaviour immediately (see below), which resulted in either successful copulation or their entering the nest of the female. Males that entered the nest of a virgin female without copulating immediately always mated successfully during the following period of cohabitation, as evidenced by females producing viable eggsacs (A. A. Maklakov, unpublished data). Thus, we considered nest entering as a successful mating event. Males were left with the females for 5 consecutive days. Each pair was fed three first-instar desert locusts on the second day of the 5-day cohabitation period.

Of 78 females, we randomly chose 39 to be presented with a second male. All second males were previously mated to one female. A second male was introduced to the female 5 days after the removal of the first male (i.e. 10 days after the first mating). We observed the pair for 3 h or until copulation occurred or the male was chased away by the female.

In *S. lineatus*, the time lag to eggsac production is highly variable and depends on female maturation time (Schneider 1999) and number of males encountered (Erez 1998). The mean time \pm SE for single-mated females of *S. lineatus* to produce an eggsac is 34.5 ± 2.1 days, and may be longer if females mate with multiple males (Erez 1998). In another study, the average time to oviposition for double-mated females was 36 and 42.2 days in 2 years (Schneider 1999). Females can remate up to 20 days after the first mating (Erez 1998), as well as after production of the first eggsac (Schneider & Lubin 1996, 1997).

We estimated male body condition by regressing male prosoma width on male body mass and using the residuals as a condition index.

Courtship Behaviour

On encounter with a female web, males initiated a searching behaviour that typically ended at the entrance of the nest ('spiral walk'). During a spiral walk males often stopped and vibrated the web with legs and abdomen. Vibration bouts consisted of one to five vibrations and could be repeated several times before the male entered the nest. Since these bouts were not very distinct, we used the total number of vibrations to estimate both vibratory

effort and vibration rate (see below). Vibrations were stereotypic and simple (unlike those of some other *Stegodyphus*, personal observations). Males that entered the nest and made physical contact with the female often left the nest, vibrated and re-entered the nest several times before copulating. The time from entering the nest to copulation ('time to mating') is variable (A. A. Maklakov, unpublished data). Copulation may occur within a few seconds, after several hours or even the following day. Males that did not copulate but were accepted by females invariably turned around and positioned themselves inside the nest facing the entrance ('face out' position). Alternatively, males could be chased away by females and leave the web. We counted the vibrations produced by a male ('vibratory effort') from the point where it discovered the web until copulation or until a male entered the nest and assumed the face out position. If a male was rejected we counted all vibrations until the male left the female's web. Vibration rate was calculated as vibrations/min $((A \times 60)/B)$, where A is vibratory effort and B is time to mating in seconds). Because males often did not vibrate at all, we also used the occurrence of vibration (yes/no) as a factor in the analyses.

Female Reproductive Success

To test for a relation between vibratory performance and female reproductive success, we kept 36 single-mated females until eggsac production and hatching of young. The females were kept individually in plastic containers as above on a standard diet (see Study Species). We recorded hatching date, number of young and the date when dispersal began. When the majority of spiderlings had left the maternal nest, about 2 weeks after the first dispersing individuals, we weighed the juvenile spiders. The following variables were used in the analysis: time to egg laying, clutch size, number of hatched young, number of dispersed young and offspring body mass. Clutch size was determined as the sum of the number of hatchlings and unhatched eggs. Dispersal was assessed visually when the spiderlings aggregated beneath the mesh-covered lid of the container. Before dispersal, the spiderlings remain in the closed maternal nest. Dispersal occurs over several weeks and depends on the size and body condition of the young (Aviram 2000). Usually, a few spiderlings initiate dispersal, which is then followed by bouts of dispersing groups that aggregate (personal observation). We removed the nest to count and weigh the young, when more than 75% of the spiderlings had dispersed. Body mass is positively related to survival in spiders (Marshall & Gittleman 1994), and mass of spiderlings at dispersal may affect their growth and final body size (Vollrath 1987). Thus, in addition to number of offspring, we used body mass at the dispersing stage as a fitness measure.

Vibration Behaviour towards Females with Eggsacs

Ten nests containing virgin females were attached to a chicken-wire fence inside a 'spider house' (a greenhouse

Table 2. The effect of male vibratory courtship, male condition and male body mass on male mating success (yes/no) with respect to female reproductive status, virgin ($N=75$) or mated ($N=39$), using two measures of vibratory performance (occurrence of vibration (yes/no) and vibration rate)

Female status	Parameter	Estimate	SE	<i>t</i>	<i>P</i>	
Virgin	Vibration (yes/no)	Constant	-3.148	1.396	-2.256	0.024
		Vibration	3.824	0.963	3.97	<0.001
		Mass	4.364	5.193	0.84	0.316
		Condition	5.353	13.747	0.389	0.697
	Vibration rate	Constant	0.874	0.738	1.184	0.236
		Rate	0.026	0.08	0.33	0.742
		Mass	-2.292	3.878	-0.591	0.555
		Condition	-7.242	10.420	-0.695	0.487
Mated	Vibration (yes/no)	Constant	-5.723	2.155	-2.655	0.008
		Vibration	0.242	0.871	0.278	0.781
		Mass	33.577	12.295	2.731	0.006
		Condition	-14.7	14.924	-0.985	0.325
	Vibration rate	Constant	-5.402	2.136	-2.53	0.011
		Rate	3.013	3.898	0.773	0.440
		Mass	31.247	12.152	2.571	0.010
		Condition	-14.332	14.667	-0.977	0.328

Mating success with virgin females refers to whether males mated within the first 3 h of observation (all males finally mated), and mating success with mated females refers to whether males mated or were chased away by a female. Statistics are from the corresponding logistic regressions.

frame, 6 × 14 m, covered with wire mesh), about 0.5 m from one another. Each female was mated to a virgin male. Females were kept in their nests until they produced eggsacs. We then presented each female with a virgin male to examine male vibratory behaviour towards females with eggsacs. The mating was carried out as described above and we recorded mating behaviour and the time to copulation for all mating pairs.

Silk-borne Cues

In this experiment we tested whether male vibratory behaviour is triggered by a silk-borne chemical cue (likely to be a sex pheromone, Suter & Renkes 1982; Schulz & Toft 1993) and whether the cue dissipates if not renewed by the female. We hypothesized that receptive virgin females produce silk-borne sex pheromones, which attract males, and that mated unreceptive females cease to renew the pheromone. We simulated this situation experimentally. Fourteen virgin females were placed in mesh-covered plastic cages and allowed to build nests and webs. We then carefully removed the females from their nests and placed them into identical cages where they could build a new nest and capture web. We tested the vibratory behaviour of males towards empty nests and webs immediately after removal of the female using the mating procedure described above. We repeated the procedure on the second and fifth day after removal of the female by placing the same males on the nests on which they had previously been placed. We compared male vibratory effort towards empty nests on the first day versus second day, first day versus fifth day, and second day versus fifth day, applying Bonferroni corrections for pairwise comparisons. On the sixth day, we removed the

virgin females from their newly built nests, and recorded male vibratory effort by placing the same males on the new nests of the same females. We then tested whether male vibratory effort was comparable to its original level (i.e. similar to the first day of the first nest). Finally, we performed an additional 23 matings with virgin spiders where females remained in their nest, to compare male vibratory behaviour towards empty and occupied nests.

Analyses

Data were analysed with SYSTAT 9. All variables were tested for normal distribution using Kolmogorov-Smirnov one-sample tests before parametric statistics were applied; when necessary, data were log transformed to obtain normality. Effects of vibration occurrence, vibration rate, male condition, male body mass and the interaction between vibration occurrence/vibration rate and condition on male mating success were analysed with logistic regression models. Nonsignificant interactions were removed and we present the outcome of the reduced models. We analysed the effect of male vibratory performance (occurrence or rate) on female fitness with linear regressions. Frequency data were analysed with tests of independence. Two-tailed *P* values are given throughout.

RESULTS

Mating with Virgin Females

All 75 pairs mated successfully regardless of whether males vibrated or not. Males vibrated towards virgin females in 57 of 75 pairs (76%; range 0–44 vibrations,

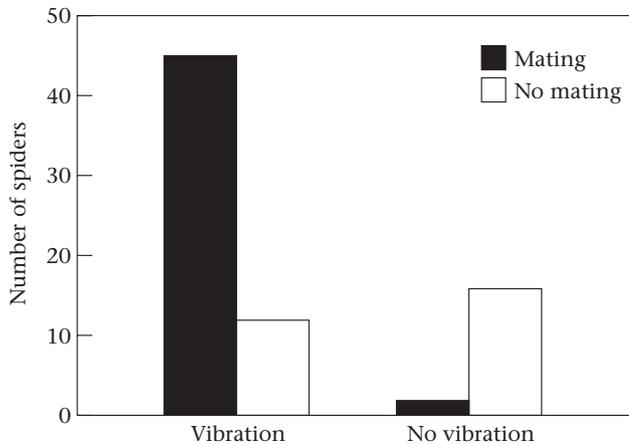


Figure 1. The effect of vibration behaviour by courting *S. lineatus* males on whether they achieved copulation within 3 h. $N=57$ vibrating males, 18 nonvibrating males.

median 4, interquartile range 0.75–14). Forty-seven pairs (62.7%) were observed mating within 3 h of presentation of the male. Vibrating males were more likely to mate within the 3-h observation period than nonvibrating males, but there was no effect of male body mass or male condition (logistic regression: log-likelihood ratio₃=29.06, $N=75$, chi-square $P<0.001$; Table 2, Fig. 1). Vibration rate had no effect on the probability of males mating within 3 h (log-likelihood ratio₃=1.575, chi-square $P=0.665$; Table 2). This suggests that vibration occurrence per se rather than the number of vibrations per time unit is important in decreasing time to mating. No interaction between male condition and vibration occurrence or vibration rate was found. For 47 pairs that mated within a 3-h period vibratory effort had no effect on time to mating (linear regression: $r=0.009$, $F_{1,45}=0.342$, $R^2<0.001$, $P=0.561$; time to mating log transformed). The duration of the first copulation event ($N=33$ mating pairs) was not significantly influenced by vibratory effort ($r=7.953$, $F_{1,31}=1.488$, $R^2<0.015$, $P=0.232$) or vibration rate ($r=-28.685$, $F_{1,31}=0.812$, $R^2<0.001$, $P=0.374$).

Mating with Mated Females

Males vibrated towards mated females in 15 of 39 pairs (38.5%), which was significantly less than the proportion of males that vibrated towards virgin females (Pearson chi-square test: $\chi^2_1=15.538$, $P<0.001$; number of vibrations: range 0–21, median 0, interquartile range 0–2). A similar result was obtained by comparing vibratory effort of 29 males towards mated and virgin females in a paired analysis: males significantly reduced their vibratory effort when presented with mated females (mated females: $\bar{X} \pm SE=1.31 \pm 0.63$; virgin females: 5.17 ± 1.35 ; Wilcoxon signed-ranks test: $Z=-2.837$, $P=0.005$; Fig. 2). Of 39 pairs of males and mated females, 22 mated (56.4%); in the other 17 cases, males were chased away or did not approach the female. Eleven of these 22 mating pairs copulated within a 3-h period. Vibrating males were not more likely to mate successfully than nonvibrating

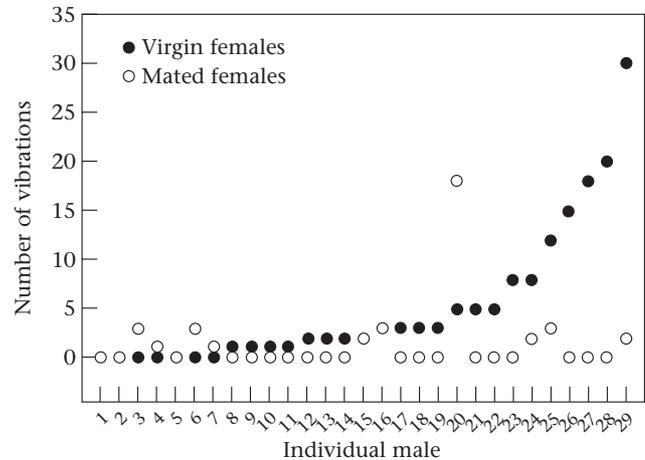


Figure 2. Pairwise comparison of the vibratory effort by 29 males courting virgin and mated females.

males and there was no effect of male condition, whereas there was a significant positive effect of male body mass on mating success (logistic regression: log-likelihood ratio₃=15.912, chi-square $P=0.001$; Table 2). A similar result was obtained using vibration rate as a measure of vibratory performance: neither vibration rate nor male condition had a significant effect on the probability of mating, whereas there was a significant positive effect of male body mass on mating success (logistic regression: log-likelihood ratio₃=16.639, chi-square P value=0.001; Table 2). There was no interaction between male condition and vibration occurrence or vibration rate. Vibratory effort also did not explain the time to mating in those males that copulated within a 3-h period (linear regression: $r=63.017$, $F_{1,9}=1.757$, $R^2=0.07$, $P=0.218$).

Female Reproductive Success

All 36 single-mated females produced viable eggsacs regardless of whether they were observed mating during the first 3 h of the mating trial. There was no effect of either male vibratory effort or vibration rate on any of the following variables: time to egg laying, clutch size, number of hatched young, number of dispersed young and offspring body mass at dispersal (Table 3). On the other hand, there was a significant effect of female body mass on all of these dependent variables.

Vibration Behaviour towards Females with Eggsacs

Male behaviour towards females with eggsacs was characterized by an almost complete lack of vibratory courtship; only two of 10 males vibrated on the web of females guarding an eggsac. Males thus vibrated significantly less towards females with eggsacs. Males thus vibrated significantly less towards females with eggsacs than towards virgin females (females with eggsacs: $\bar{X} \pm SE=1.2 \pm 3.04$ times; virgin females: 8.3 ± 2.32 times; Wilcoxon signed-ranks test: $T=54$, $N=10$, $P=0.002$). This result is similar to that obtained for mated females without eggsacs (see

Table 3. The effect of total number of premating vibrations (vibratory effort) and vibration rate produced by courting *S. lineatus* males on female fitness, measured as time to oviposition, clutch size, number of hatched young, number of dispersed young and mean offspring body mass

Dependent variables	Explanatory variables	df	Standardized coefficient	SE	t	P
Vibratory effort						
Time to oviposition	Vibratory effort	2	<0.001	0.106	0.746	0.461
	Female mass	2	-0.379	7.52	-2.358	0.024
Clutch size	Vibratory effort	2	-0.158	0.219	-1.240	0.224
	Female mass	2	0.648	15.609	5.080	<0.001
Hatched young	Vibratory effort	2	-0.045	0.198	-0.293	0.772
	Female mass	2	0.47	14.105	3.023	0.005
Dispersed young	Vibratory effort	2	-0.059	0.201	-0.373	0.712
	Female mass	2	0.446	14.323	2.832	0.008
Offspring body mass	Vibratory effort	2	-0.055	<0.001	-0.374	0.710
	Female mass	2	0.549	0.001	3.744	0.001
Vibration rate						
Time to oviposition	Vibration rate	2	-0.084	0.29	-0.521	0.606
	Female mass	2	-0.415	7.508	-2.583	0.014
Clutch size	Vibration rate	2	0.017	0.613	0.129	0.898
	Female mass	2	0.68	15.870	5.246	<0.001
Hatched young	Vibration rate	2	0.025	0.542	0.163	0.871
	Female mass	2	0.482	14.035	3.119	0.004
Dispersed young	Vibration rate	2	0.044	0.550	0.279	0.782
	Female mass	2	0.463	14.252	2.960	0.006
Offspring body mass	Vibration rate	2	0.049	<0.001	0.334	0.740
	Female mass	2	0.567	0.001	3.887	<0.001

Statistics are from corresponding linear regressions. See text for details.

above). When we compared male vibration behaviour on the webs of mated females with and without eggsacs, there was no significant difference in male vibratory effort (Mann-Whitney U test: $U=166$, $N_1=10$, $N_2=39$, $P=0.397$).

Silk-borne Cues

Male vibratory behaviour towards nests from which a virgin female had recently been removed was similar to that towards nests occupied by virgin females (Mann-

Whitney U test: $U=117.5$, $N_1=14$, $N_2=23$, $P=0.171$). Males had reduced their vibratory effort by the second day after removal of the female (day 1: $\bar{X} \pm \text{SE}=5.14 \pm 1.27$ times; day 2: 2.71 ± 1.1 times; Wilcoxon signed-ranks test with Bonferroni correction: $T=61$, $N=14$, $P=0.015$; Fig. 3). On the fifth day, they also vibrated less than on the first day (1.21 ± 0.58 times; $T=77$, $N=14$, $P=0.003$) but the difference between second and fifth days was not significant ($T=37.5$, $N=14$, $P=0.098$). When presented with the newly constructed nests of the same females (after the female was removed), males increased their vibratory effort to the initial level (3.71 ± 1.03 times; difference between fifth day and new nest: $T=55$, $N=14$, $P=0.004$; difference between first day and new nest: $T=46.5$, $N=14$, $P=0.139$).

DISCUSSION

There was a large variation in the vibration behaviour of *S. lineatus* males towards both virgin and mated females. Premating vibration was not a prerequisite for successful mating. Thus, all males mated successfully with virgin females, although 24% did not produce premating vibrations. When males were presented with mated females, the proportion of vibrating males and their vibration effort was less than in experiments with virgin females. In the light of these results, it appears that species recognition and predation suppression are not the primary functions of courtship vibrations in *S. lineatus*. Both of these hypotheses, which may be functionally indistinguishable (Suter & Renkes 1982), assume that courtship functions as a male identity signal. Identity signalling implies standardized courtship as a prerequisite that enables a female

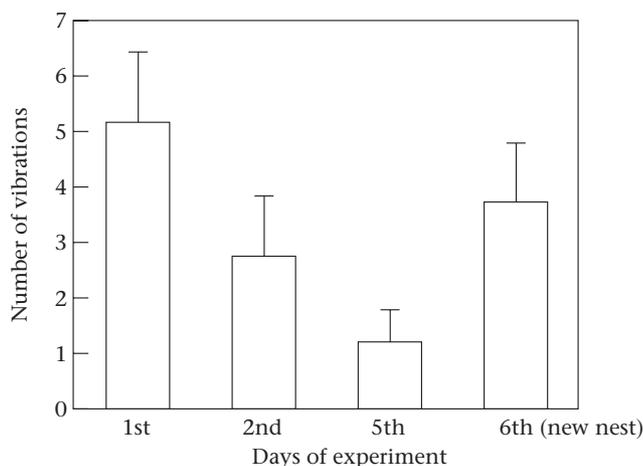


Figure 3. Number of vibrations \pm SE produced by *S. lineatus* males on empty female webs on the first, second and fifth days after the female was removed. Male behaviour on the newly built nest of the same female ('new nest') was used to control for habituation.

(mated or virgin) to recognize the courting spider as a conspecific or a male, and this was not found in our experiments.

The quality-signalling hypothesis predicts that females will be selective and will base their choice on a male trait that correlates with male quality. We found that virgin *S. lineatus* females mated indiscriminately, while only 56.4% of mated females accepted a second male. Consequently, we expected males to increase their vibratory effort when confronted with mated females, and females to base their choice on male vibratory effort. However, males vibrated more often towards 'indiscriminate' virgin than 'resistant' mated females and vibrating males were not more likely to mate with 'resistant' females than nonvibrating ones. The reduction of male vibratory effort in a situation where female choice is likely to occur strongly suggests that vibrations are not a quality signal in *S. lineatus*. Furthermore, we found no effect of male vibratory effort or vibration rate on female fitness correlates such as time to egg laying, clutch size, number of hatched young, number of dispersed young and offspring body mass. We conclude that there is currently no evidence that male premating vibration in *S. lineatus* functions as a male quality signal selected via female choice. It is possible that vibrations transmit information at a level that could not be detected by our observational methods or that female spiders can preferentially use sperm from the best courting males. Nevertheless, the facts that vibrations are not necessary for successful courtship to occur even when the female has received sperm (i.e. is mated), and that there is a decrease in vibratory courtship towards mated females, argue against the signalling role of vibratory courtship in *S. lineatus*.

Male body mass had a positive effect on male mating success with mated females. This result is consistent with that reported for a desert spider *Agelenopsis aperta*, and it is possible that females prefer heavier males as mates if it increases the success of their offspring (Singer & Riechert 1995). Alternatively, heavy males may be more successful in fighting with nonreceptive females (sensu Schneider & Lubin 1996, 1997; Erez 1998). To answer these questions, the net short- and long-term costs and benefits of female multiple mating must be taken into account. There was no effect of male body condition on male mating success, and also no significant interaction between body condition and vibratory performance. These results suggest that vibration ability is not condition dependent and correspond with the finding that factors other than vibratory performance, for example body mass, influence male mating success.

Copulation duration may influence sperm transfer (Parker 1998) or sperm uptake by the female (Bukowski & Christenson 1997). We found no effect of male vibratory effort on the duration of the first copulation in *S. lineatus*, but the possibility remains that vibratory effort may influence fertilization success. However, the acceptance of the second male by a mated female was not based on vibratory effort. Consequently, rejected males were denied the opportunity to influence vibratory-based sperm use by females.

We suggest that vibratory male courtship in *S. lineatus* functions primarily to stimulate the female to copulate by assuming a mating position. It is not necessary for males to vibrate for copulation to occur; nevertheless, vibrating males mated faster with virgin females, which supports the female stimulation hypothesis. Why then, do males not always vibrate? Male vibratory reaction may be triggered by a sex pheromone produced by a receptive female to attract males. Communication through sex pheromones is common in spiders (Olive 1982; Suter & Renkes 1982; Watson 1986; Schulz & Toft 1993; Prenter et al. 1994). Our data show that males initiated courtship when presented with a female web from which the female had been removed. Furthermore, male vibration behaviour on the empty web decreased with time suggesting that the silk-borne cue needs to be renewed by the female. Vibration behaviour was restored to its original level when males were presented with a fresh female web, further suggesting renewal of a silk-borne pheromone. There is a possibility that males habituated to a particular web. However, this hypothesis implies that males remembered the structure of the particular web, which we consider unlikely. Thus, it appears that male courtship behaviour is triggered by a female sex pheromone. Possibly, some of the virgin females had not produced male-attracting pheromone at the time of our experiment and males reacted by entering the female's nest without initiating a proper courtship. Such behaviour is common in this species, and *S. lineatus* males even cohabit with subadult conspecifics in nature (Schneider 1997).

Male vibration behaviour on the old abandoned webs resembled that on the webs of mated females and of females with eggsacs. We suggest that once females become unreceptive after mating, they cease to produce sex pheromone, which results in a reduction of male vibratory courtship.

In conclusion, we found no evidence that premating vibrations produced by *S. lineatus* males provide an opportunity for sexual selection via female choice. The data also contradict the hypotheses that vibrations are species- or sex-specific recognition signals. We suggest that the primary function of this behaviour is to stimulate receptive (virgin) females to assume the mating position and copulate. Male vibrating behaviour does not stimulate nonreceptive females.

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