

Female silk and mate attraction in a burrowing wolf-spider (Araneae, Lycosidae)

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Summary

Female silk triggers male searching, trail-following or courting in most spider species. This response is extremely sex-specific, hence it is suggested that silk helps males to recognise and/or locate conspecific females. Several lines of evidence indicate that this function is partially accomplished by a sex-pheromone bound to the female silk. In a burrowing wolf-spider (*Lycosa tarentula fasciiventris* Dufour, 1835) we analysed the role of female silk in the recognition and location of potential mates, as well as the existence of such a sex-pheromone. Only adult virgin females actively lay draglines in the vicinity of their burrow. Male response to these lines (searching, trail-following, courting and silk laying) is stereotyped but not highly specific, as it also appears upon contact with burrow silk or with heterospecific draglines. Moreover, female draglines do not increase the likelihood of males finding female burrows. Water, but not time, reduces but does not eliminate dragline effectiveness as a sexual releaser, which indicates the existence of a minimally volatile, somewhat water-soluble chemical bound to the silk. We conclude that female draglines provide tactochemical signals informing male burrowing wolf-spiders about the presence and reproductive condition of a female. They mediate mate recognition but not location, so they could function as a way of promoting sexual selection.

Introduction

Most spiders are solitary animals, which face the problem of meeting a conspecific for reproduction. Female silk is involved in solving this problem in both web-building and non web-building species, as male behaviour is modified upon contact with it in the vast majority of species and environmental conditions so far studied (for reviews see Tietjen & Rovner, 1982; Pollard *et al.*, 1987). Male response may be specific, including courtship, searching and trail-following (Tietjen, 1977; Tietjen & Rovner, 1980; Roland, 1984) or not, involving changes in the locomotion rate or the orientation of the male (Suter & Renkes, 1982; Rovner, 1991). Silk thus fulfils the requirements to be considered a substratum that carries information involved in courtship communication (Wilson, 1975; Krebs & Dawkins, 1984).

There is no consistency in results reporting the species-specificity of this signal. Males of some species respond both to conspecific and to heterospecific female silk (Tietjen & Rovner, 1982; Roland, 1984; Barth & Schmitt, 1991) and others do not (Hegdekar & Dondale, 1969). This discrepancy may be attributed to experimental design, as males prefer conspecific silk when given the choice (Roland, 1984), but this preference does not necessarily entail following the conspecific thread (Barth & Schmitt, 1991). Silk may thus lack the species-specificity needed for it to be considered a substratum involved in species recognition (Tietjen & Rovner, 1982; Barth, 1993).

On the other hand, in all but a few exceptions, courtship is released only by the adult female silk but not by that of males (Tietjen, 1977; Jackson, 1987; Arnqvist, 1992) or subadult females (Jackson, 1987; Anava & Lubin, 1993). This sex-specificity has been generally interpreted as indicating the existence of silk-bound sex-pheromones (for a review see Pollard *et al.*, 1987), which have been demonstrated to be involved either in male orientation (Dijkstra, 1976) or sexual arousal (Hegdekar & Dondale, 1969). This last possibility is especially appealing in the case of stationary female spiders, as they could use silk to release male courtship and so increase their likelihood of gathering information about male quality (Anava & Lubin, 1993) or species identity (Barth & Schmitt, 1991; Barth, 1993).

However, this may not necessarily be the case in lycosids, where males are not the only wandering sex (Foelix, 1996); nonetheless, there are a few burrowing lycosids. Compared with a number of studies dealing with the role of female draglines in mate attraction in wandering genera (*Rabidosa*: Tietjen, 1977; Tietjen & Rovner, 1980; *Pardosa*: Hegdekar & Dondale, 1969; Dondale & Hegdekar, 1973; Dijkstra, 1976; *Schizocosa*: Hegdekar & Dondale, 1969) there is as yet almost no information concerning burrowing lycosids. In the only previous study, the probability that these species (e.g. *Geolycosa*) use draglines for attracting mates was considered unlikely (Miller & Miller, 1986, 1987).

Lycosa tarentula fasciiventris Dufour, 1835, is a Mediterranean wolf-spider inhabiting dry and open areas with herbaceous vegetation. Adult females are obligate burrowers, and adult males wander around in search of them. Maturation takes place in late spring, and reproduction occurs shortly afterwards before males completely disappear from natural populations. Pairs mate inside the female's burrow, and females may mate more than once with different males (pers. obs.). Males thus have to locate conspecific females in an extremely short time period. Burrow silk or female draglines could help them as either sexual releasers or sexual attractants. In this paper we explore these possibilities.

Material and methods

Experiments were conducted in the laboratory between 1995 and 1998. The spiders (the numbers of individuals are given separately for each experiment) were captured as immatures in the field at Cantoblanco (Madrid, central Spain) and kept in the laboratory until death. They were individually caged and visually isolated from each other under constant conditions (L:D 12:12, 25°C, water and food supplied twice a week). Maintenance cages (6.5 × 12 cm wide, 17 cm high) were filled with 7 cm-deep soil, where we made an artificial burrow. The spiders usually habituated to the cages and rebuilt and maintained their burrows as they do in the wild. They were checked for moulting daily, and size was measured as the width of the exuvial prosoma. Females were used for trials either in their penultimate instar (S) or as adults (A), and ages were calculated as days since last moulting. Most females were virgin (AV), but some

mated in the laboratory before testing (AM). Males (MA) were all adult and virgin. In order to ensure independence of data, every animal was usually used only once in the same experiment. If not, successive trials were separated by at least three days for males and seven for females.

In the first experiment, designed to analyse the relationship between dragline laying behaviour and female reproductive condition (developmental stage, age and reproductive status) we built circular experimental terraria (42 cm diameter). Walls were of transparent plastic (40 cm high) and the bottom was filled with soil (18 cm deep) with an artificial cylindrical burrow (3 cm in diameter and 10 cm deep) in its centre. The surface of the soil was covered with black cardboard, which was replaced for every test. A female was transferred to the burrow and allowed to move freely in the terrarium for at least 24 hours. Afterwards we checked whether or not there were any draglines on the soil surface. In order to improve visual assessment of draglines, we placed on the cardboard 16 small stones arranged so that they formed two concentric circles of eight regularly spaced stones each, 10 and 20 cm away from the burrow.

In the first experimental series, females of any reproductive condition ($n=17$, age 78.41 ± 90.55 days) remained in these terraria for 6 days, and were checked for the presence of draglines on an irregular schedule. We analysed if the probability of dragline laying changed from day to day (Kruskal-Wallis test). In a second experimental series, to test for differences in dragline laying depending on the female's developmental stage and reproductive state, we included data collected only on the first day and tested additional S ($n=13$), AV ($n=15$), and AM females ($n=8$). We compared the occurrence of silk-laying among these groups (Chi-square test).

In a third experimental series we used only AV females. They remained in the experimental terraria from their maturation day until they started to lay silk, the presence of which was checked daily from the first day on. Females were randomly assigned to an experimental condition: no male presence ($n=19$), meaning that they were always alone in the terrarium, or male presence ($n=13$), meaning that a male was presented every day and the pair allowed to interact for 30 minutes. We recorded the age at which females in these two groups started to lay draglines and tested for differences between groups by the Mann-Whitney test.

A second experiment was designed to analyse whether and how female draglines modify the behaviour of conspecific males. AV females were removed from the experimental terraria after 24 hours. The presence and location of draglines were noted and a conspecific male ($n=27$, age 24.12 ± 20.43 days) immediately put on the terrarium surface. Male response was videotaped (JVC TK-C621 video-camera, JVC SVHS HR-S7000 video-recorder, FOR-A VTG 55 video-timer) for 10 minutes. From the videotapes we described the patterns of male behaviour and whether or not males were able to orient towards the female burrow. We tested for dependence between male behaviour and female draglines (Chi-

square test) and used a binomial test to compare the probability of males orienting to the female burrow with that expected at random.

In a third experiment we tested the specificity of the male response. In the first experimental series we placed clean filter papers (25 cm^2) in the female and male maintenance cages. Twenty-four hours later these filter papers were used as a stimulus in the floor of a clean plastic cage ($49.5 \times 24.5 \times 14 \text{ cm}$ in size) to which a conspecific male was transferred. We videotaped the male's behaviour for 10 minutes following contact with the filter paper, and compared (Chi-square test) the number of males reacting positively to it depending on its type of origin: (1) AM ($n=15$ males, age 42.12 ± 18.28 days), (2) AV ($n=22$ males, age 37.93 ± 26.7 days), (3) S ($n=21$ males, age 50.63 ± 14.7 days), (4) MA ($n=16$ males, age 36.06 ± 20.47 days) and (5) clean cages (CO) ($n=21$ males, age 47.06 ± 19.36 days). The effect of male condition was tested immediately afterwards by allowing males to contact AV draglines. Non-responding males were excluded from the analysis.

In the second experimental series draglines were provided by AV females of a closely related species (*Lycosa* sp., Parellada, 1998). We used the same experimental set-up as in the first experiment and checked for the presence of draglines on the terrarium surface 24 hours after adding the female. Immediately upon removing the female an adult male *L. t. fasciiventris* was placed in the terrarium ($n=6$, age 37.67 ± 17.01 days) and its response videotaped for 10 minutes. We recorded the number of males responding positively to the heterospecific female silk and tested for the dependence between this response and the presence of draglines by the Chi-square test.

A fourth experiment was designed to test for the effectiveness of silk other than draglines (e.g. burrow silk) as a male sexual releaser. We carefully extracted silk from the maintenance burrows and used it as the stimulus in glass terraria (20 cm diameter, 11 cm high) to which a conspecific adult male was transferred. The

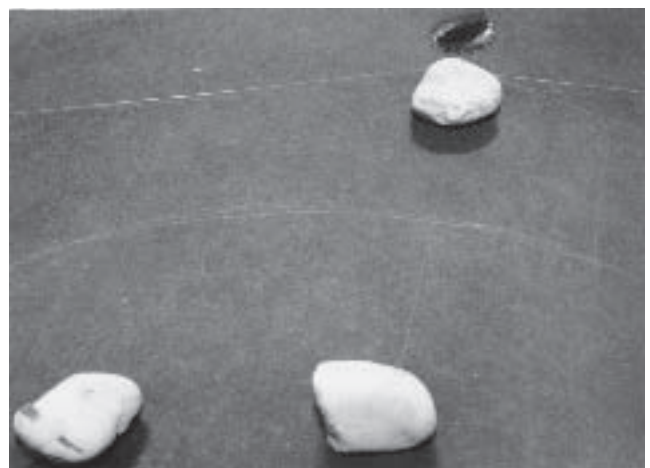


Fig. 1: General appearance of draglines laid by adult and virgin females in our experiments. Females suspended draglines in the air and tightened them by fixing them from place to place, usually to the stones.

	Yes	No	Total
AM	1	7	8
AV	30	2	32
S	0	13	13
Total	31	22	53

Table 1: Results of experiment 1, second series, showing the number of females laying draglines relative to their developmental stage (A=adult, S=subadult) and reproductive status (M=mated, V=virgin).

behaviour of the male was videotaped for 10 minutes after contact with the silk. We recorded the number of males responding to AV ($n=10$ males, age 22.8 ± 13.16 days) and S ($n=6$ males, age 31.33 ± 22.59 days) burrow silk and tested for dependence by the Chi-square test. The effect of male condition was checked as in the previous experiment. Additionally we mounted a dragline and a portion of subadult burrow silk for examination under SEM (Philips XL 30, SIDI, UAM).

Our last experiment was designed to test for the persistency of draglines as sexual releasers. In order to best imitate natural conditions we tested the effect both of time and of water. For this purpose filter papers (25 cm^2) which had been placed in the maintenance cages of AV females for 24 hours were experimentally treated and their effectiveness as male sexual releasers tested afterwards in the same experimental set-up as in experiment 3. In the first experimental series ($n=22$ males, age 63.64 ± 30 days), treatment consisted of leaving the filter paper in an open box at room temperature for a period of between 3 and 45 days. In the second experimental series we either sprayed water ($n=13$ males, age 45.69 ± 15.41 days) or immersed the filter paper in water for 30 minutes ($n=15$ males, age 37.13 ± 11.40 days). Afterwards the filter papers were allowed to dry at room temperature for 24 hours. The effect of male condition was checked as above and the Chi-square test was used to test the effect of filter treatment on the probability of male response.

Results

In experiment 1, many females actively laid draglines. As attachment points they mostly used the stones we

had placed on the cardboard (Fig. 1). When draglines were laid, a single night was enough: in the first experimental series, all females that laid draglines and which were checked daily ($n=9$, age 9.0 ± 2.92 days) had shown this behaviour after a single night. The identity of the individual lines and the amount of segments laid down showed a slight variation from day to day, which suggests that females actively maintained their signalling system. However, differences in the number of dragline segments produced were not statistically significant (Kruskal-Wallis test: $\chi^2_5=1.22$, $p=0.9427$).

Female developmental stage and reproductive status explained individual differences in dragline laying behaviour, which was typically shown only by virgin adults (Table 1; Chi-square test: $\chi^2_2=41.67$, $p=0.00000$, contingency coefficient: $C=0.6635$). Age of females was also important, as dragline laying did not appear immediately upon reaching adulthood but 2–8 days later ($n=32$, age 4.56 ± 1.69 days, Kolmogorov-Smirnov $Z=1.098$, $p=0.179$). On the other hand, the presence of conspecific males had no significant effect on the mean age of first dragline production (4.87 ± 1.46 days, $n=13$, and 4.42 ± 1.80 days, $n=19$, for females tested with and without males, respectively, Mann-Whitney test: $U=59.5$, $p=0.3691$).

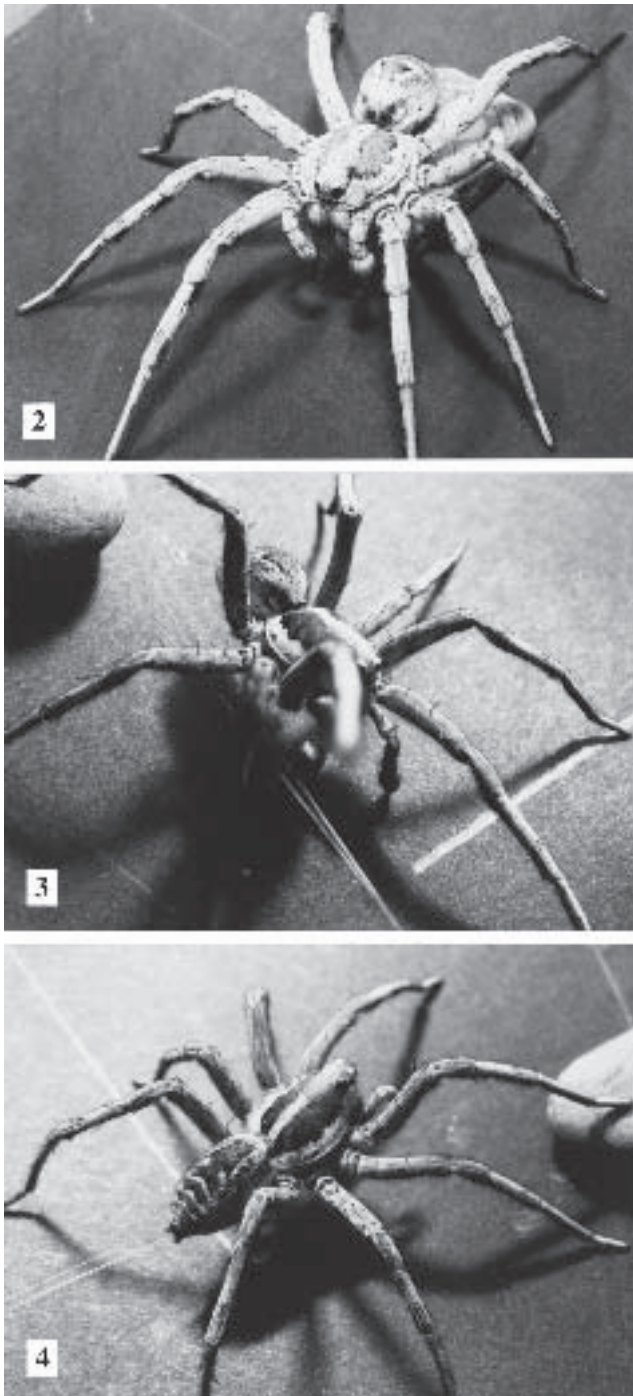
In experiment 2, males showed a set of highly stereotyped behavioural patterns almost immediately upon contact with female draglines (Table 2). These behaviours were a response to draglines, as they never occurred when no draglines were present ($n=11$), and they occurred 90.91% of times ($n=33$) upon contact with draglines (Chi-square test: $\chi^2_1=31.43$, $p=0.0000$; $C=0.6455$). Male behaviour in the absence of draglines consisted of withdrawing to the periphery of the terrarium or remaining in one spot. On the contrary, male response to female draglines included a series of leg and pedipalpal movements while the male straddled the dragline (**trail-following**, Figs. 2, 3). Occasionally, males **laid** their own **dragline** (Fig. 4) over the female's while following it, which caused the latter to become attached to the substrate. **Courtship**, as well as some less stereotyped palpal and foreleg movements (**substrate exploration**) were interspersed with trail-following and were never performed directly on the dragline but on the substrate. Trail-following and courtship were usually

Behavioural pattern	Description
Trail-following (Figs. 2, 3)	The male straddles the female dragline and moves forwards. Pedipalpal tarsi contact female silk at their dorsal surface or tip. Forelegs are flexed and may also contact silk. Foreleg and pedipalpal movements on the dragline are diverse, going from sliding to tapping or dragging the thread, which causes a variable degree of silk displacement. Usually one of the pedipalps maintains contact while the other moves downwards and forwards and then upwards and backwards.
Dragline laying (Fig. 4)	Male opisthosoma moves left and right while the male straddles the female dragline and moves forwards. While so doing the male lays his own dragline on top of the female's. This movement gives rise to a final zigzag shape of the thread.
Substrate exploration	The tips or the dorsal surface of the pedipalpal tarsi are in contact with the substrate. Pedipalps rotate quickly and alternately on the substrate, backwards and medially, and forwards and laterally.
Foreleg sweeping	The male remains in one spot without contact with the female dragline. Foreleg tarsi slip backwards while resting on the substrate, causing forelegs to bend at the femur-patella and tibia-metatarsus joints.

Table 2: Results of experiment 2, listing the patterns of male behaviour shown after contact with conspecific female draglines, with brief descriptions. Male response mainly involved movements of the pedipalps and forelegs, and consisted of **trail-following**, **dragline-laying** and **substrate exploration**.

performed at a distance (about 10 cm) from the female burrow, and the probability of males orienting to the burrow did not differ from random (Binomial test: $p=0.5078$, $n=9$).

In experiment 3, only filter papers from AV female cages were partially or completely covered by silk. Males explored and courted in response to these substrates as they had to female draglines, likewise doing so almost immediately upon contact. Subadult and already mated females released these responses in a significantly lower number of cases (Chi-square test: $\chi^2_4=124.91$,



Figs. 2-4: Behavioural patterns shown by adult male *Lycosa tarentula fasciiventris* upon contact with female draglines. **2, 3** Trail-following, showing two different positions of the pedipalps; **4** Male laying his own dragline on top of the female's.

	Yes	No	Total
AM	0	24	24
AV	37	1	38
S	2	29	31
MA	0	23	23
CO	0	23	23
Total	39	100	139

Table 3: Results of experiment 3, showing the number of males responding by courting or exploring the substrate (Yes) to filter papers from the substrate of conspecifics differing in sex, developmental stage and reproductive status (AM= adult mated female, AV=adult virgin female, S=subadult female, MA=adult male, CO=control).

$p=0.00000$; $C=0.6880$), which suggests that the male response is specific to AV female silk (Table 3).

Adult *Lycosa* sp. females showed the same dragline laying behaviour as *L. t. fasciiventris* and males responded to heterospecific draglines as they had to conspecific draglines, by exploring the substrate, trail-following and courting. The occurrence of such a response was exclusively attributable to the presence of draglines, as it never appeared when there were no heterospecific draglines ($n=2$), whereas it was shown by all males ($n=4$) upon contact with heterospecific draglines.

In experiment 4, some males reacted to female burrow silk by courting or exploring the substrate, but the effectiveness of this silk was lower than that of draglines (70%, $n=10$, and 50%, $n=6$ of males responded to AV and S burrow silk, respectively). Correspondingly, the probability of male response did not depend on female developmental stage (Chi-square test: $\chi^2_1=0.64$, $p=0.42371$, NS). Therefore, males may exploit burrow silk for finding potential mates regardless of the physical differences between dragline and burrow silk (Figs. 5, 6), but they do not use burrow silk to discriminate the developmental condition of the female.

Experiment 5 showed that time had no effect on silk effectiveness. Filter papers continued to elicit the response of every male tested, whatever the time that had elapsed since the draglines were laid (Chi-square test: $\chi^2_1=0.5888$, NS). On the other hand, water treatment significantly reduced silk effectiveness. Water-treated filter papers elicited sexual behaviour in a significantly lower number of males, and this effect was stronger when water was applied by immersion than by spraying (Table 4; Chi-square test: $\chi^2_2=18.84$, $p=0.00008$; $C=0.4713$).

Discussion

The results summarised here show that female silk acts as a sexual releaser for *Lycosa tarentula fasciiventris* courtship, probably by means of a sex-pheromone. Although the role of female silk in sexual communication is widely documented in this family (reviewed in Tietjen & Rovner, 1982), in this burrowing species we have found evidence of both the active placement of

	Yes	No	Total
No treatment	37	1	38
Spray	10	3	13
Immersion	7	8	15
Total	54	12	66

Table 4: Results of experiment 5, summarising the number of males that responded by courting or exploring the substrate (Yes) to filter papers previously treated with water under one of two treatment conditions (spray or immersion).

draglines by females and the incidental usage of burrow silk by males. Burrow silk informs males only about the presence of conspecific females, whereas draglines also signal the females' readiness to mate. These different uses of silk by a single species had previously been explored only by Suter & Renkes (1982). Our results also show male dragline laying in response to female draglines, something not described previously.

The first conclusion was supported by several facts. First, dragline laying behaviour was almost restricted to AV females, and we know that the receptivity of female *L. t. fasciiventris* is strongly dependent on female reproductive condition (Fernández-Montraveta & Ortega, 1990). Secondly, dragline laying behaviour was time-limited, and its occurrence was dependent on female age and mating history, in contrast to some other species (Hegdekar & Dondale, 1969). This result was not a side-effect of a lack of males in our laboratory, as it was not modified when conspecific males were present. Thirdly, during the period of dragline production, females actively maintained their draglines. Finally, male behaviour was significantly modified upon contact with conspecific draglines, and this response was extremely stereotyped.

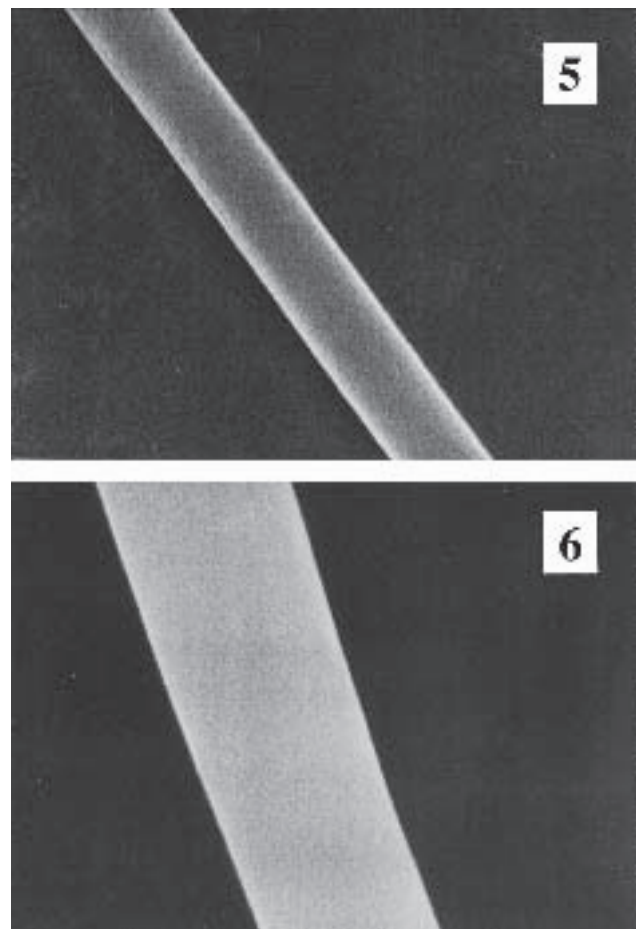
The male response involved behavioural patterns which are remarkably similar to those described in other lycosids (*Lycosa rabida* Walckenaer and *L. punctulata* Hentz: Tietjen, 1977; Tietjen & Rovner, 1980, which have since been transferred to the genus *Rabidosa* by Brady & McKinley, 1994). Tietjen (1977) used the term "trail-following" to describe these behaviours and interpreted them as indicating a reliance on chemical and, to a limited extent, mechanical cues to guide males towards females. Others (e.g. Dijkstra, 1976) also had found that orientation was mostly chemically based. In our experiments on a burrowing lycosid, trail-following did not significantly help males to orient towards female burrows, and this reduces the likelihood of draglines mediating male orientation either chemically or mechanically. On the contrary, contact with female draglines elicited searching and courting in an area close to the female burrow, where males spent most of the observation time. As a result, we hypothesise that female draglines of this burrowing lycosid serve to increase the time males spend in activities near the female burrow.

Female *L. t. fasciiventris* play an active role during sexual interactions by approaching and contacting courting males (Ortega-Escobar *et al.*, 1994). Therefore our results support the view that signalling by females is a mechanism of increasing their likelihood of gathering

information about male quality (Anava & Lubin, 1993; Uetz *et al.*, 1996) or species identity (Barth, 1993). Alternatively we hypothesise that signalling by draglines might increase the number of males present in the neighbourhood of the burrow at any given time (Watson, 1990).

Of course there are alternative interpretations for our results. If draglines were designed to reduce searching time and there was the risk of exploitation by competitors or predators, they would also lack any accuracy in indicating the precise location of the burrow. Support in favour or against any of these hypotheses will be forthcoming from field information about the duration of the reproductive period, the availability of potential mates and the reliance of predators on silk for finding female burrows.

In any case, other results support our interpretation. First is the silk laying behaviour shown by males. Such a behaviour could be explained as a way of reducing the probability of competing males locating females by means of draglines. This hypothesis has already been demonstrated in spiders (e.g. *Linyphia litigiosa* Keyserling (Linyphiidae): Watson, 1986, where male behaviour (web-reduction) reduces the probability of competing males locating females, and *Schizocosa ocreata* (Hentz): Ayyagari & Tietjen, 1987, where



Figs. 5–6: Micrographs ($\times 15,000$) showing the microsculpture of female *Lycosa tarentula fasciiventris* silk. **5** Dragline laid by an adult virgin female; **6** Silk from the burrow of a subadult female.

male silk carries a pheromone inhibiting other males). Secondly, male response was unspecific. Responding both to adult and subadult female silk would be difficult to understand in terms of male benefit if adult female silk was highly effective in reducing searching time. On the contrary, as female *L. t. fasciiventris* occupy their burrows permanently and moult inside, it would be advantageous to males to behave opportunistically and not only search for females ready to mate but also locate subadult female burrows and wait for females to moult. Cohabitation has been demonstrated in other burrowing wolf spiders (*Geolycosa turricola* (Treat): Miller & Miller, 1987) and is also documented in *L. t. fasciiventris* natural populations, though to an extremely variable extent (pers. obs., J. Moya-Laraño, pers. comm.).

Lack of specificity in male response regardless of physical differences between female draglines and burrow silk, together with the reduction of signal effectiveness by water dilution, point to the existence of a water-soluble sex-pheromone in *L. t. fasciiventris*. As time had no effect on signal effectiveness, it is probably a contact sex-pheromone (Hegdekar & Dondale, 1969). Its effectiveness did not disappear completely after water treatment as in previously studied temperate zone lycosids (Dondale & Hegdekar, 1973; Tietjen, 1977). This suggests that pheromones used by this burrowing lycosid may be adapted for some degree of water resistance, as has been found to be the case in lycosids inhabiting tropical rain-forests (Lizotte & Rovner, 1989).

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