

Mate guarding in two *Linyphia* species (Araneae: Linyphiidae)

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Summary

Precopulatory mate guarding is described for *Linyphia tenuipalpis* Simon and *L. triangularis* (Clerck). Adult males appear in the webs of subadult females one or two days before the females' final moult. Mating takes place immediately after the moult. Nearly all females are guarded; even if not, they are mated within about two days. Larger males have greater mating success than smaller males. Both males and females may mate more than once. If two males compete for access to the same female, the subordinate male can prevent mating between the female and the dominant male by interference. Mating interference is considered an alternative to fighting as a male reproductive strategy in small males.

Introduction

This paper describes precopulatory mate guarding in *Linyphia tenuipalpis* Simon and *L. triangularis* (Clerck), based on direct observations of field populations. Mate guarding is the behaviour by which a male associates with a female for a period of time longer than necessary for copulation and defends this association against rival males, in order to assure paternity to at least some of the offspring of that female. The phenomenon is known in a wide range of animals, including arthropods (review in Thornhill & Alcock, 1983).

In the spider literature descriptive terms, like 'cohabitation' (Jackson, 1978, 1986) or the 'suitor phenomenon' (Robinson & Robinson, 1978; Robinson, 1982), have been applied to behaviours interpreted as part of a precopulatory mate guarding strategy (Austad, 1984). In most cases males guard subadult females, and mating takes place soon after the female becomes adult. Though probably widespread among linyphiids (cf. Watson, 1986; Suter & Keiley, 1984; Austad, 1984) few detailed accounts are available. Rovner (1968) studied the sexual behaviour of *L. triangularis* and described 'web sharing' for up to two days, but seemingly did not observe mate guarding.

Material

Linyphia triangularis is one of the most abundant and well-known spiders in most of Europe (Helsdingen, 1969), occurring in several kinds of habitats. *L. tenuipalpis* is a more restricted species; in Denmark it is confined to *Calluna* heaths (Toft, 1980). In this habitat, the two species occur together, occupying identical niches at the same time (Toft, 1987, and this study). Adult females of both species may invade webs of the other species, evict the owner and take possession of the web (Toft, 1987). The study was initiated by the

idea that, because of interspecific web take-overs, chemical signals on the silk might give confusing messages to males about the identity of the female web-owner. My field observations did not confirm the existence of such a problem, probably because matings occur mainly at a time when web take-overs may be less frequent.

Copulation in *Linyphia* follows the typical linyphiid pattern (Helsdingen, 1965; Austad, 1982). It starts with a series of intromissions before sperm induction (phase A), then the male spins a sperm web and fills his palps with sperm, followed by a new series of intromissions (phase B). The whole sequence of phase B (sperm web spinning, sperm induction and intromissions) may be repeated several times. Sperm are transferred to the female only during phase B.

Austad (1982) found that the linyphiid *Frontinella pyramitela* (Walck.) had "first male priority", i.e. if the female mates several times the first male will father most of the offspring. Both mate guarding and male-male fights must be considered from this perspective (Austad, 1984).

Study area and methods

Field observations were made during the 1987 season (August-September) on the heaths belonging to the Mols Laboratory in Eastern Jutland, Denmark. The study site was situated on a southeast sloping hill with patches of heather, *Calluna vulgaris* L., mingled with areas of bare sand interspersed with tufts of the low grass *Corynephorus canescens* (L.). *Linyphia* spiders placed their webs only in the heather, but were easy to observe and manipulate from the bare sand without causing disturbance. An area of 12 × 8 m was staked out, and every web was marked with a small numbered flag. From 14 August all adult males encountered in this area were collected, anaesthetised with carbon dioxide and marked individually with painted dots on the femora. Three measures of size were taken, namely cephalothorax length, cephalothorax width and tibia I length, all measured under a binocular microscope, and the animals were released again at the point of collection. Marking of females was not feasible in this study, since observations covered a moult. The area was scanned approximately twice daily during the female moulting period 18 to 28 August, after which strong winds for several days destroyed all webs. The stage (subadult/adult) of females and identity of males were noted on each sighting. Supplementary observations of matings, male fights, feeding and other behaviours were made.

The mating status of adult females in the population was analysed by dissection. About ten individuals of each species were collected from the heather adjacent to the observation area every two days in the early part of the adult phase, and additionally several times during the rest of the adult season. After being deeply narcotised with carbon dioxide, their spermathecae were dissected free, cut open in a drop of physiological salt solution, and the preparation observed through a phase-contrast microscope.

Results

Mate guarding

There were no observable differences between the two species in general guarding and mating behaviour, so unspecified descriptions in the following sections will cover both species.

Adult males of *L. tenuipalpis* were observed for the first time on 12 August, those of *L. triangularis* two days later. The course of events during the ten-day observation period can be seen from Fig. 1. In both species the females go through their final moult within this period, the species being only 2-3 days out of phase. Males become mature about one week earlier than females, and nearly all males have become adult when the first adult females appear. By comparing numbers of subadult females with subsequent numbers of adults it is seen that there is a strong immigration of *L. tenuipalpis* into the observation area, while there is a decrease (emigration?) in *L. triangularis*.

The number of males observed in the area reaches a peak and levels out again before all females have moulted. In *L. tenuipalpis* increased male numbers coincide with the peak of female moults, while in *L. triangularis* male numbers fluctuate more. It is further observed that in *L. triangularis* moulting is more synchronised than in *L. tenuipalpis*.

As females were not marked it was impossible to follow the history of those individuals that did not stay in the same web. For 26 females of *L. tenuipalpis* and

11 females of *L. triangularis*, the exact date of moulting was recorded as well as presence of males in their webs in the days preceding and/or following the moult (Fig. 2). In *L. tenuipalpis* presence of males shows a clear peak on the day before the female moult. In *L. triangularis* again the pattern is less clear-cut. However, in both species male presence is concentrated into 2-3 days before and 2-3 days following the female moult.

Females may be guarded by one, two or three males. The intensity of pre-moult guarding in *L. tenuipalpis* is higher than in *L. triangularis* (Fig. 2). Thus in the latter species 6 out of 10 females, whose guarding history was known with certainty, were not guarded on the day before the moult, while in the former the comparable figures were 4 out of 18 ($p = 0.057$, Fisher's exact probability test). Also, the incidence of a female being guarded by more than one male was higher in *L. tenuipalpis*, tending to augment the difference when expressed as in Fig. 2.

If a female is guarded mating takes place immediately following the moult, when she is still pale in colour. The male starts active courting the moment she returns to the web. The female accepts the male with no sign of aggression, there being no indication of female choice. After completion of the mating sequence the male soon leaves the web. This explains the drop in guarding intensity in *L. tenuipalpis* on the day of the moult: females mated early in the day were not guarded at the time of observation.

Observations later in the season show that males persist in the population until the females lay eggs and disappear in early October. However, the incidence of males in the web of a particular female remains low for the rest of her life.

Males arriving at the web of a subadult female may stay and guard or they may leave. No males seem to stay by a female for more than two days before her moult. In *L. tenuipalpis* 4 males out of 5 stayed after arriving two days before the female moult, while nearly all males arriving one day before the moult stayed, unless challenged by other males.

Nearly all females are guarded at the time of their moult. In *L. tenuipalpis* only two females out of 26 under observation showed no sign of sexual activity, either by the presence of males or sperm webs, on the day of moulting. However, in one case mating was postponed by more than one day as a result of male fighting (see below). In *L. triangularis* male activity and matings occurred until two days after the female moult, but by that time nearly all females seem to have been mated.

These behavioural observations indicate that an adult female in the field is likely to be mated. Results of the dissections show that this conclusion is valid (Table 1).

For *L. tenuipalpis* the data allowed the evaluation of the importance of male size for the success of guarding. There was no difference in the size distribution of the total male population and those observed guarding (defined as present in female webs on the day before and the day of moulting).

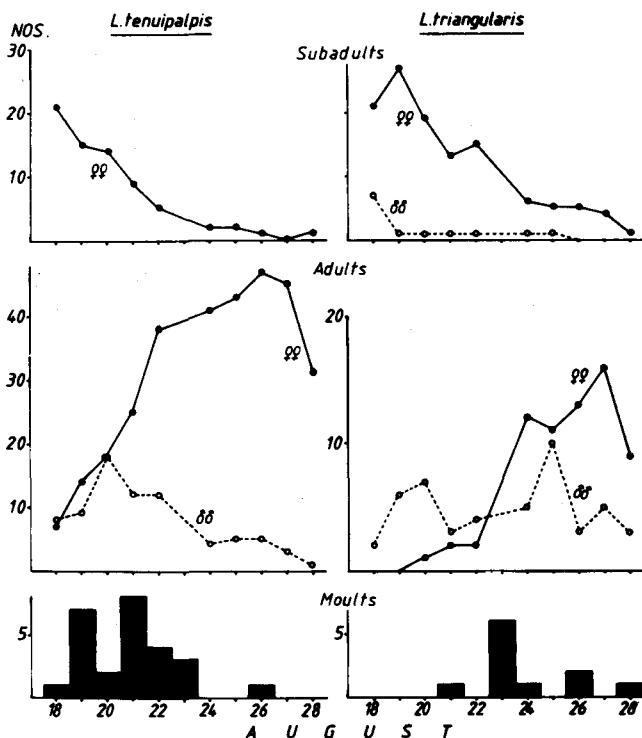


Fig. 1: Graphs: Changes in the populations of *Linyphia tenuipalpis* and *L. triangularis* in the study area, during the period when the females moult into the adult stage (August 1987). Figures for males include those in their own webs (subadults and recently moulted adults), in female webs and outside webs; females are all web-holders.
Histograms: Distribution of recorded female moults.

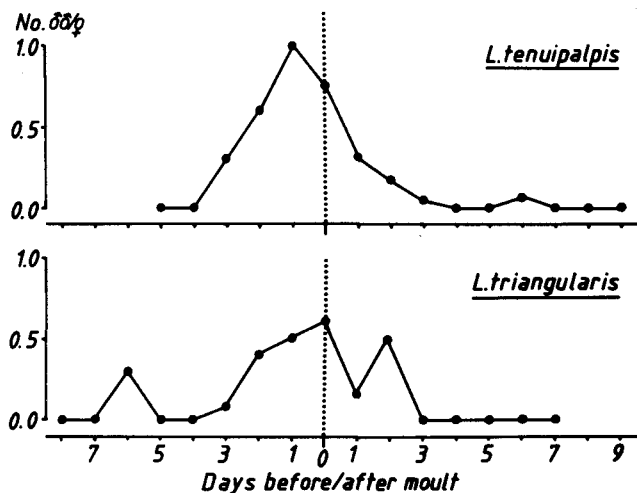


Fig. 2: Number of guarding males per female web in relation to the day of female moult into the adult stage. Webs may be guarded by 0, 1, 2 or 3 males.

However, of guarding males those observed mating were significantly larger (cephalothorax length) than those not observed mating (Mann-Whitney U-test, $p < 0.05$, one-tailed). From laboratory studies on *L. triangularis* it is known that males have sperm capacity for 1-2 matings per day for the 10-day period (Toft, unpublished). Therefore, the size distribution of males would not be expected to change very much. In agreement with this, no trend was discernible in the data.

Behaviour during guarding

After the males have completed their final moult they appear in the subadult females' webs to feed. Here the males are dominant and are able to secure for themselves most of the prey hitting the web (a similar situation was described by Rovner (1968) for the females' adult period). Later, when females approach their moult, the males seem to feed less. During the period of guarding the web usually becomes smaller and may be only a few cm² at the time of the moult. There may be two reasons for this. First, the females stop repairing the web, which then deteriorates. Secondly, males may actively reduce the web (cf. Helsdingen, 1965; Rovner, 1968). I have not directly observed this last behaviour in the field, but the rate of decrease in web size indicates that it does take place. However, the immediate and complete reduction of webs by males upon entering, as described from laboratory observations, was not seen in the field here.

Because of web reduction before moulting and mating, many females have to start a new web after becoming adult. For this reason there is a high incidence of change in web sites at this time.

When males arrive at the web of a subadult female they initiate behaviours associated with courtship: 'abdominal jerking', 'palpal drumming', etc. Usually the female withdraws and takes up a position at the margin of the web. In one case, however, a female *L. tenuipalpis* on the day before her moult, behaved

'receptive' and the pair performed a seemingly perfect sequence of copulation behaviours, during which the male applied his palps to the epigynal area of the female. This 'pseudocopulation' was continued for at least three hours.

Multiple mate guarding

Several cases of interference between males were observed. Male fights have been described in detail by other authors (Rovner, 1968; Austad, 1983; Suter & Keiley, 1984). In general my observations agree with their results on the point that larger males are dominant over smaller males during aggressive encounters. However, although a larger male may displace a smaller male and take over the guarding position in the web sheet, the mating opportunity is not thereby assured. In several cases the displaced male was able to interfere with the sexual activities of the female and the dominant male. During normal mating sequences the act of mating is easily interrupted by sudden disturbances of the web, for example by a prey insect (Rovner, 1968; own observations). The same happens when a second male enters the web during the mating. Thus a displaced male may prevent the displacer from obtaining the mating by interference. Two extensive observations with *L. tenuipalpis* indicate that this is not unusual. In both cases the displaced male succeeded in preventing the mating between the female and the dominant male for several hours. In one of these cases the dominant male disappeared after four hours of chasing, with the result that the smaller male obtained the mating.

These two cases agreed in another interesting aspect, namely that the displaced male made no attempt to interfere with the activities of the mating pair as long as they were in phase A. However, as soon as the dominant male started to make his first sperm web, the second male rushed into the web, approaching the female.

During the present study mating interference by a second male was observed only in *L. tenuipalpis*. Later observations show this behaviour also in *L. triangularis* (N. Nielsen, pers. comm.).

	<i>L. triangularis</i>	<i>L. tenuipalpis</i>
18 August		10/11
20 August		17/17
22 August	5/5	13/13
24 August	11/11	10/10
26 August	10/11	10/10
28 August	10/10	8/8
3 September	13/13	14/14
17 September	15/15	9/9
Total	64/65	91/92

Table 1: Mating status of adult females of *Linyphia triangularis* and *L. tenuipalpis* during the adult season 1987. Figures indicate numbers with spermatozoa in spermathecae/total numbers dissected.

Multiple mating

Contrary to the statement of Rovner (1968) regarding *L. triangularis*, females of *L. tenuipalpis* may mate with more than one partner. Thus, two females were observed in copulation 5 and 8 days after their first mating, respectively. Four other females of unknown, but more than two or three days' adult age, were seen copulating. Remating by females has been reported for several related species (Austad, 1982; Martyniuk & Jaenike, 1982; Suter & Renkes, 1984; Watson, 1986).

Males too, may mate with more than one female. Two *L. tenuipalpis* males were observed in copulation with different females only one day apart, and a third male at three days interval.

Discussion

Though Rovner (1968) studied *L. triangularis* both in the laboratory and in the field, he did not observe the mate guarding behaviour described here. The main reason for this is that his field work was performed during the period after the spiders had become adult, as he specifically mentions. This may also be the reason for his statement that females copulate only once. My observations indicate that most rematings also take place within a week or so following the moult. Though some males persist for the remainder of the female season, it is extremely rare to see a copulation at a later time. Thus the number of matings performed by female *Linyphia* spiders certainly is limited. In *Frontinella*, females are claimed to be always receptive (Suter & Renkes, 1984).

Though my data for *L. triangularis* are scanty, it seems safe to conclude that a smaller fraction of *L. triangularis* females were guarded at the time of moulting than was the case for *L. tenuipalpis*. This resulted in the finding of more females which were not mated until about one or two days after their moult. It is reasonable to hypothesise that the difference originated in the different degree of synchronisation in moulting between the two populations. As there is a normal 50:50 sex ratio among subadults (own observations), and males are probably continuously sexually active, the operational sex ratio will be skewed to the male side, the more so the less the females are synchronised.

Nothing is known about the sperm priority pattern of these *Linyphia* species. However, all behaviours seen are consistent with the 'first male priority' found in another linyphiid (Austad, 1984). Guarding of subadult females clearly results in the guarding male becoming the female's first mating partner. Also the peculiar pattern of interference behaviour displayed by subordinate males, attempts to prevent another male from mating first. The change in the behaviour of the subordinate male at the moment the dominant male starts sperm web spinning is so abrupt, from motionless attending to fast intruding, that he seems to be fully 'aware' of the fact that this is a last call for interference. Actually, his response is so fast, that in the cases observed the dominant male failed to even initiate

sperm induction.

To judge from these observations the subordinate male is able to monitor the behaviours performed by the dominant male, probably by reading the pattern of web vibrations produced by these behaviours. Vollrath (1979) demonstrated that the kleptoparasitic spider *Argyrodes* is able to recognise and respond to specific web vibrations produced by prey-swathing by its araneid host. It is likely that male *Linyphia* recognise and respond to the particular vibration pattern associated with sperm web spinning.

The dynamics of combat among male spiders has been studied extensively in recent years (Christenson & Goist, 1979; Vollrath, 1980; Austad, 1983; Suter & Keiley, 1984). Combat is an effective strategy in male-male competition for access to females, but only for the larger of the two. According to Austad (1983) a displaced *Frontinella* male waits at the web periphery until the dominant male has finished mating; then he enters and remates the female. In view of the established sperm priority pattern (Austad, 1982), the benefit of this behaviour in terms of fertilisations cannot be very great. My observations here suggest a different alternative strategy in *Linyphia* pertaining to the smaller male of a competing pair: persistent interference. It seems that a small male can prevent a larger male from completing sperm induction and initiating phase B mating, with little risk to himself, as long as he keeps away from direct combat. The outcome of this kind of competition may then be determined by factors different from those of combat. One possibility might be considerations about when to give up the chasing runs resulting from interference. A relevant consideration may be the chances of finding and gaining access to another unmated female, if the present one is relinquished. All other things being equal, these chances will probably always be higher for a large male than for a small one: by his probably higher walking speed he will find a new female faster, and by his larger size he will have a better chance of displacing a possible new competitor. Time considerations might induce a giving-up decision sooner in larger than in smaller males, thus making interference a profitable strategy for smaller males. However, the larger size of males observed mating compared with those not observed mating, indicates an overall size advantage.

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