

Approach Strategy by which Male Mediterranean Tarantulas Adjust to the Cannibalistic Behaviour of Females

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Abstract

In sexually cannibalistic species, selection is thought to have favoured the evolution of male approaching behaviour that reduces the probability that the female will kill the male. However, investigations of behaviours that could reduce the probability of sexual cannibalism are few. We examine the hypothesis that male wolf spiders, *Lycosa tarantula* (L.) (Araneae, Lycosidae), decides to approach females in periods when they are less dangerous. Males of this species approach females for mating during the daytime only. While attending females, males stay farther from the female's burrow at night than during the daytime. In field experiments, we offered a grasshopper (typical prey) or a male *L. tarantula* to females at night and during the day, and our findings show that the diel changes in the male's approaching behaviour matches diurnal changes in the female's tendency to attack both the grasshopper and the male spider. These findings support our hypothesis that a diel change in female responsiveness to prey has been a selection pressure influencing the evolution of male approach behaviour in a sexually cannibalistic species.

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Introduction

Differences in strategies by which males and females maximize fitness can result in sexual conflict (Andersson 1994; Chapman et al. 2003). The conflict of interest between the sexes can be extreme in spiders, because in many species females can kill and subsequently feed upon the males (Elgar 1992; Schneider & Lubin 1998). Males must approach females in order to mate, but may also need to adopt precautions against being preyed upon by their potential partners. Females, by practising sexual cannibalism, may gain additional offspring from the meal

obtained by feeding on males, but they also risk remaining unmated when cannibalism occurs before copulation.

It has been argued that, in sexually cannibalistic species, morphological and behavioural traits have evolved in response to selection imposed by sexual cannibalism (Darwin 1871; Pycraft 1914; reviews in Bristowe 1958; Platnick 1971; Robinson 1982; Elgar 1992). For example, males of a Mediterranean mantid, *Iris oratoria*, are less willing to mate when forced to approach females from the front, directly exposing them to her raptorial legs, than if they are allowed to approach from the rear (Maxwell 1999). Similarly, in some web-spinning spiders, males approach females primarily when they are feeding (Robinson 1982), an activity during which they are less aggressive than at other times (Prenter et al. 1994).

The Mediterranean tarantula *Lycosa tarantula* (L.) is a burrowing wolf spider in which males and females are similar in size and in which the female is known to be cannibalistic (Fabre 1913; Fernández-Montraveta & Ortega 1990; Moya-Laraño et al. 2002; Moya-Laraño 2002). Males, which are approx. 10× larger than the most common heterospecific prey (Moya-Laraño et al. 2002), are potentially a profitable meal for a female. Sexual cannibalism may thus aid female *L. tarantula* in compensating for a limited food supply (Moya-Laraño et al. 2002, 2003a, b) as males can account for up to 30% of the biomass intake of females (Moya-Laraño et al. 2002).

In a phylogenetically diverse set of spiders, adult male spiders cohabit with subadult females (i.e. one instar from maturation) until the females reach maturity (Jackson 1986). This behaviour may reflect mate-guarding tendencies (i.e. males guard females until the latter mature in order to gain a paternity advantage) (Austad 1984; Elgar 1998), as demonstrated in a web-weaving spider (Fahey & Elgar 1997). Despite the risk of sexual cannibalism, cohabitation between males and females occurs in burrowing wolf spiders (Miller & Miller 1986), including the Mediterranean tarantula (Moya-Laraño et al. 2003a,b). Cohabitation in this spider is probably a form of mate guarding as fights occur between males when more than one discovers the pheromone-marked silk dragline with which females encircle their burrows. The first male to find the cue is more likely to win the contest (Fernández-Montraveta & Ortega 1993). The pattern of cohabitation in Mediterranean tarantulas appears to reflect the risk of sexual cannibalism. Cohabiting males remain at a distance from the burrow of a subadult, or recently moulted mature females, until mating occurs. Males may remain near a female's burrow for as long as 3 d, approaching the female to mate only during the day and depart, if they survive the encounter, immediately afterwards (Moya-Laraño et al. 2003b).

Adult females search for prey at night either by sitting at the burrow's mouth (sit-and-wait foraging) or as far as 1 m from their burrows (active foraging) (Moya-Laraño 2002). The fact that mating occurs only during the day, when females are not actively hunting, suggests that natural selection has favoured males that approach and court a female only during daylight hours when they may be less predatory. If the risk to the male of sexual cannibalism is higher at night than during the daytime, then we predict that males will stay farther away

from the female's burrow at night. Our hypothesis is that females are more dangerous at night because this is when they are more responsive to prey. Mistaken identity (i.e. when the female cannot distinguish a male from other prey) (Elgar 1992) is unlikely to be the reason for this, as spiders tend to have acute ability to discriminate conspecific individuals from other organisms (e.g. Jackson 1985; Clark & Jackson 1995; Foelix 1996). What we propose is, instead, that the female is in a predatory state at night and this spills over into how they respond to males, making them more dangerous. Hence, in addition to determining changes in the female's tendency to attack typical prey, we also examined the female tendency to prey on males, and determined whether or not a male's chances of escaping cannibalism are higher if it approaches a female during the daytime than at night. We report our findings here.

Methods

The study site is located in desert grassland (Cabo de Gata, Almería, Spain) (for details, see: Moya-Laraño et al. 2002, 2003b). The research was conducted within the mating season of *L. tarantula* (1–30 June 1997).

Documentation of Diurnal Changes in Cohabitation Distances

During the first 4 d we measured and marked 60 subadult females (i.e. females that were one moult from reaching maturation). Each spider was first immobilized in a fine mesh. After measuring the spider's carapace and abdomen widths and giving it a code identifying it as an individual (enamel paint was used to mark legs), we released the spider into her burrow (for details, see: Moya-Laraño et al. 1996, 2002; Moya-Laraño 1999, 2002). Females were measured and marked again after they had moulted to adulthood. All females were visited once from 10.00 to 16.00 hours every day for 28 d, and once between 10.00 and 15.00 hours every other night for 16 nights. In each visit, we searched for males in the vicinity of the female's burrow. Each newly encountered male was captured, marked and released in the location where it was found. In each visit we measured the distance from the burrow for both newly discovered and previously marked males. Our criterion for considering whether cohabiting was taking place was finding a male near a female's burrow on two consecutive visits, i.e. once during daylight and also at night. Because the distribution of the difference between day/night distances was not normal (Zar 1996), we used the non-parametric Wilcoxon matched-pairs test for comparing the distances of males from females.

Field Experiment 1: Female Tendency to Attack Prey

Grasshoppers (*Oedipoda* sp.), which are considerably smaller than *L. tarantula* males (approx. one-third of the male weight), were caught in the study area and dropped singly into female burrows during daylight (between

10.00 and 11.00 hours) or at night (between 22.00 and 23.00 hours). We tested 10 females (five at night, five during the day) on 24 June, and 10 more on 25 June. Two trials in which the grasshopper jumped outside the burrow after being introduced were repeated with different grasshoppers and spiders. For each female, we recorded whether or not the grasshopper was caught within 5 s. This gave us an index of the female's tendency to attack prey. We chose such a short observational period to measure responsiveness towards prey because *L. tarantula*, like some other lycosids (e.g. Marshall 1996), is a visual hunter that responds immediately to moving prey within a short range.

Field Experiment 2: Female Aggressiveness Towards Males and Male Survival

Trials were performed on two consecutive days with different males and females. Males were captured 12–24 h before the trials and were randomly assigned to either day or night trials. We released a different male at the mouth of the burrow of 20 adult females during the day (from 10.00 to 14.00 hours) and at the burrow of 10 different females during the night (from 22.00 to 01.00 hours). There were fewer trials at night because we expected cannibalism to occur more frequently at night and we wanted to minimize depletion of the male population. The male was released at the edge of the female's burrow using a plunger to slowly force him to exit a 15-mm-diameter opaque tube (see Moya-Laraño et al. 2002). The male had the choice of either entering the burrow or walking away. In three cases, the male left and we started over with a different male and a different burrow. All instances of males being reluctant to enter a burrow were at night. Trials were terminated when the male was forced from the burrow, was cannibalized, or after 15 min if neither had occurred. Males that leave the burrow within the 15-min test period can do so after a female has either rejected or unsuccessfully attacked them. In our field observations, simple rejection could be distinguished from an unsuccessful attack. The former involved the female gently pushing the male away, with the female never leaving her burrow to chase the male, whereas an attacking female jumped on top of the male and even left the burrow to chase him. Those trials that did last the full 15 min ended either with the male at the burrow entrance or inside the burrow.

Because the experiment was conducted towards the end of the mating season (21–22 June), most females likely had already mated. However, females are still courted by males at this time (Moya-Laraño et al. 2003b).

Results

Documentation of Diurnal Changes in Cohabitation Distances

Cohabiting males tended to stay more than 4× farther from the female's burrow at night than during the day (Fig. 1a; Wilcoxon matched-pairs test, $n = 24$, $Z = 3.86$, $p = 0.0001$). During the night cohabiting males maintained their

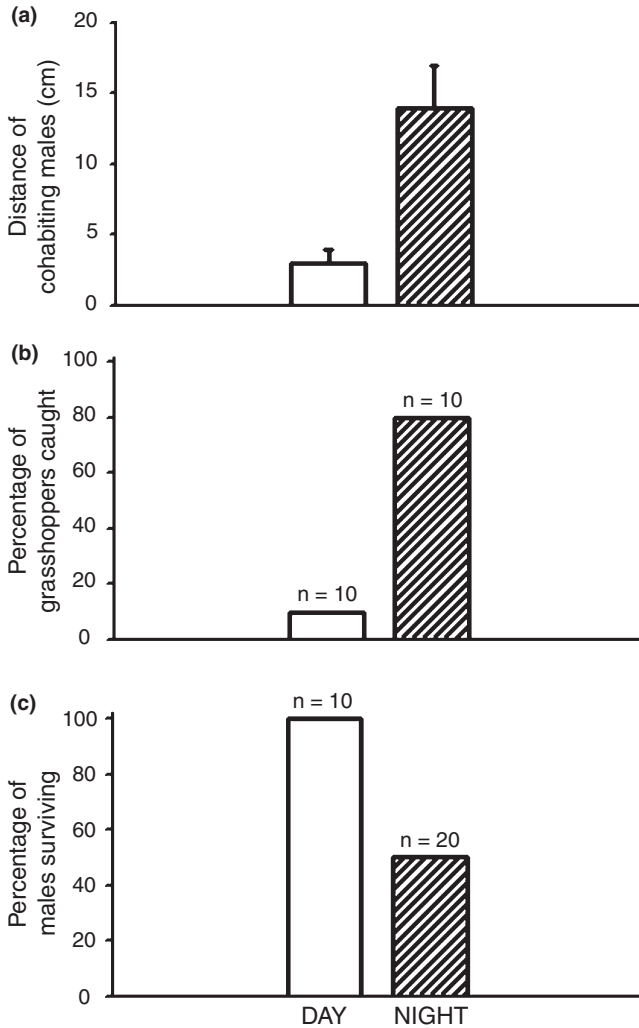


Fig. 1. (a) Distance from females (\pm SE) at which cohabiting males were found ($n = 24$) in daytime and at night. Males were approx. $4\times$ farther from the burrow at night. (b) Females were more likely to attack grasshoppers dropped inside the burrow at night. (c) Males had a greater chance of surviving sexual cannibalism in encounters induced during daytime than at night. Numbers on above the bars indicate sample sizes (see text for statistical analyses)

bodies in contact with the ground, with their legs completely extended. During the day, males were found mating inside the female's burrow in approx. 25% of the visits. The male's legs were never extended if he was beside or on top of the burrow during daytime.

Field Experiment 1: Female's Tendency to Attack Prey

Females were much more responsive to prey at night: 80% of the introduced grasshoppers at night were preyed on, but only 10% were preyed on during the day (Fig. 1b; $G_1 = 11.02$, $p = 0.0009$).

Field Experiment 2: Female Aggressiveness Towards Males and Male Survival

Females rejected males by gently pushing them away at a higher rate during daylight (12/20) than at night (0/10) ($G_1 = 13.46$, $p = 0.0002$), and tended to attack them more often at night (6/10) than during daylight (2/20) ($G_1 = 8.33$, $p = 0.0039$). None of our induced encounters ended in mating. None of the males that entered the burrow during the day was killed, but 50% of those that entered at night were cannibalized by the female (Fig. 1c; $G_1 = 13.17$, $p = 0.0003$).

Discussion

Our observations indicate that *L. tarantula* mates only during the daytime (Moya-Laraño et al. 2003b). Our data show an additional diel pattern: (1) cohabiting male *L. tarantula* are approx. 4× as far from the female's burrow at night than during daytime; (2) at night, the male's posture is different; (3) female *L. tarantula* are more responsive towards introduced prey at night than during the day; (4) at night, females also behave more aggressively towards males that enter the burrow; (5) males are more often cannibalized by females if they enter the burrow during the night time instead of the daytime. These parallel diel behavioural patterns are consistent with our hypothesis that natural selection has favoured males that avoid approaching females at night because females are more responsive to prey at that time and therefore also are more dangerous to males at night than during the daytime.

We do not know what cues males use for avoiding females at night. A potential candidate is a female behaviour, which may act as a proximate factor that discourages males from approaching too close to their burrows at night. Adult females place a pheromone-marked 20-cm circle of silk around their burrows that males can recognize (Fernández-Montraveta & Ruano-Bellido 2000). Perhaps males use this as a perimeter beyond which they should not approach at night.

Alternative hypotheses, not related to sexual cannibalism, might explain why males stay farther from the burrow at night. Males could be closer to the burrow in daytime in order to be closer to shelter from predators and solar radiation. One could also hypothesize that males position themselves farther from the burrow at night in order to increase their chances of finding prey by reducing competition for food with a foraging female. This last hypothesis is unlikely because, as in most spiders (Givens 1978; Foelix 1996), the foraging rate of mature *L. tarantula* males is much lower than that of females (J. Moya-Laraño, unpubl. data). These hypotheses and ours are not mutually exclusive.

Female aggression is known to change across the mating season in sexually cannibalistic species (Elgar 1992). Once females have obtained sufficient sperm to fertilize most of their eggs, aggression towards males may change because the male's value as sperm donors has decreased relative to his value as a meal. This switch must be especially stronger in *L. tarantula*, where males have a relatively high nutritious value compared with other prey in the environment (Moya-Laraño et al. 2002). Our second experiment was conducted at the end of the mating season, when the population is comprised mostly of mated females, which are the most aggressive towards males (Carmen Fernández-Montraveta, pers. comm.). Thus, the rate of female attack we observed is likely the maximum in the season. Nevertheless, there exists a marked difference in female aggressiveness between night and day at the end of the mating season.

In conclusion, a diel change in female responsiveness towards prey in *L. tarantula* is correlated with changes in the distance of cohabiting males from the female burrow, the rate at which females attack males, and male mortality from sexual cannibalism. This pattern suggests that males stay away from female burrows at night in order to reduce the risk of cannibalism. Thus, our results are consistent with the hypothesis that a diel change in female aggressiveness has been one factor shaping the evolution of male approaching behaviours in a cannibalistic species.

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