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TERRITORIALITY IN A CANNIBALISTIC BURROWING WOLF SPIDER

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Abstract. Field experiments to test the hypothesis that a cannibalistic species is territorial are rare. We conducted two field experiments to test the hypothesis that adult females of the Mediterranean tarantula, *Lycosa tarentula* (L.) are territorial. In a relatively long-term experiment we placed a female intruder in an artificial burrow within the hypothesized territory of a resident. The intruders disappeared from their burrows at 7× the rate of spiders in a reference and two control treatments. Residency status, not relative size, determined whether the intruder or the resident remained, and evidence suggests that the winner frequently cannibalized the loser. We also conducted a short-term field experiment in which we induced encounters between females. The results were consistent with territorial defense because escalation was more likely if spiders were similar in size, and cannibalism, the outcome of one-third of the encounters, occurred only after escalation. Thus, adult females of the Mediterranean tarantula are territorial, and cannibalism may be a consequence of territorial defense.

Key words: burrowing wolf spiders; cannibalism; cannibalistic territoriality; fatal fighting; field experiments; Lycosa tarentula; *territoriality.*

INTRODUCTION

Cannibalistic animals can eliminate potentially competing conspecifics by both territoriality, i.e., the defense of a fixed area in excess of a central place (i.e., burrow, nest) resulting in the exclusion of conspecifics from that area (Maher and Lott 1995), and/or by cannibalism. As a consequence, in species exhibiting both behaviors, territoriality is difficult to establish without focused experimentation, because territoriality and simple cannibalism can produce similar spatial patterns in the population (Dong and Polis 1992, Marshall 1996, Gordon 1997) and food scarcity increases both the rate of cannibalism (Polis 1981, Dong and Polis 1992, Wagner and Wise 1996, 1997, Samu et al. 1999) and the intensity of territorial behavior (Brown 1964, Schoener 1983). Because the costs and benefits of the two behaviors are substantially different (Dong and Polis 1992, Stamps 1994), distinguishing between the behaviors in natural populations may help to understand their evolution and impact on natural communities. Despite the potential importance of territoriality and cannibalism in generalist predators, field experiments proving territoriality in cannibalistic species are rare.

Arachnids, which often are food limited (Wise 1993) and can be both territorial and cannibalistic (Riechert 1982, Polis 1990), are ideal candidates for testing the hypothesis of territoriality in cannibalistic species. Cannibalism appears to be widespread among wolf spiders, both burrowing and nonburrowing species (Fabre 1913, Edgar 1969, Hallander 1970, Fernández-Montraveta and Ortega 1990, 1991, Wagner and Wise 1996, 1997, Samu et al. 1999). Burrowing wolf spiders are particularly attractive for such a test, because they exhibit regular spacing (Riechert 1982, Fernández-Montraveta et al. 1991, Moya-Laraño et al. 1996, Marshall 1997), intraspecific interference competition (Marshall 1996, Moya-Laraño et al. 1996), burrow-site tenacity (Fernández-Montraveta et al. 1991, Moya-Laraño et al. 1996), fights over burrows that may end in cannibalism (Fernández-Montraveta and Ortega 1990, 1991), and travel farther from the burrow if they are in poor condition (Moya-Laraño et al. 1998). Therefore, cannibalism and territoriality may occur simultaneously in burrowing wolf spiders.

The Mediterranean tarantula, *Lycosa tarentula* (L.), a well-studied burrowing wolf spider, is cannibalistic and exhibits patterns consistent with the hypothesis of territoriality (Fernández-Montraveta and Ortega 1990,

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1991, Moya-Laraño et al. 1996, 1998, Moya-Laraño 1999). We employed field experimentation to test directly for territoriality in the Mediterranean tarantula and determined how cannibalism relates to territorial defense.

METHODS

Our field experiments were conducted during July and August 1997 in the Natural Park of Cabo de Gata-Níjar in Almería, Spain, on a 30-ha section of flat desert grassland with scattered shrubs (*Thymelaea hirsuta* L.) and *Nassella tenuissima* (Trin.) as the predominant grass cover. Cabo de Gata, with $<$200 mm of rain per year, is the most arid mediterranean zone in Europe (Peinado et al. 1992).

Experiment 1: testing for territorial exclusion

We experimentally created intruders, without directly inducing encounters, by introducing adult females in artificial burrows into the hypothesized territory of a neighbor. The artificial burrow consisted of a 10 × 10 cm piece of PVC pipe, which was placed in the soil and filled with fine sand. A small amount of water was used to compact the sand, and a stick was used to fashion an artificial burrow of 2 cm in diameter inside the PVC pipe. Some burrowing wolf spiders, including *L. tarentula*, build a turret around their burrow using debris and silk (Wallace 1942, Ortega 1986). The original turret from the natural burrow in which the spider was living was removed and carefully placed on top of the artificial burrow. This procedure was done because the turret may substantially improve survival in burrowing wolf spiders (Shook 1978). Spiders in artificial burrows laid down silk for fixing the turret to the burrow and further excavated the burrow to one side within the first 24 h of settlement. Spiders were not confined for days in the artificial burrow before the experiment started, but they were rather changed from their natural burrow to the artificial burrow when the replicate was set up.

We first identified pairs of natural nearest neighbors by locating a female-occupied burrow, the resident spider, and then finding her nearest neighbor, the spider that would become the intruder, designated the focal individual. The resident was captured, measured, marked, and released back into her burrow (Moya-Laraño et al. 1996). The intruder was also measured and marked, but was released into the artificial burrow. In order to ensure that the intruder was placed within the hypothesized territory of the resident, we first measured the nearest neighbor distances of 55 randomly selected occupied burrows and found that the minimum nearest neighbor distance (MNND) in this sample was 65 cm. Intruder burrows were then located at half this distance (32.5 cm) from the burrow of the resident spider. Because MNND/2 was the estimated radius of the smallest territory in the population, spiders that were moved to this distance from the spider designated as the resident were likely to have been placed within that spider's territory. This manipulation (TER) constituted the direct test of territoriality. A reference treatment (REF) was established for comparison. In REF a spider designated as the ''resident'' and its natural nearest neighbor, designated the ''focal'' individual, were captured, marked, and released back into their original burrows. The response of the focal individual was compared with that of the intruder, i.e., the focal individual, in the TER treatment.

Two additional treatments were established to control for possible consequences of the TER manipulation unrelated to territorial exclusion. In addition to being placed within the hypothesized territory of the resident, the intruder spider in the TER treatment experienced a change from a natural burrow to an artificial one, and displacement from its selected burrow site to another one. These two manipulations could potentially affect the future use of space of the intruder female independently of territorial interactions, either because she abandoned the artificial burrow because it did not match her shelter requirements, or because she abandoned the new site because it did not match her microhabitat requirements. To account for these two possibly confounding effects, we used pairs of spiders designated ''residents'' and ''focal individuals,'' selected as in TER and REF treatments, to establish two control treatments: (1) CONB, control for artificial burrow, in which the focal individual was placed in an artificial burrow in the position of her natural burrow; and (2) CONS, control for change of burrow site, in which the focal individual was placed in an artificial burrow 32.5 cm from the burrow of the resident as in the TER treatment but the resident spider and her burrow turret were then removed and her burrow was filled with sand. All spiders were measured (carapace width and abdomen width) and marked before being released into their respective burrows. The sum of carapace and abdomen widths accurately predicts the mass of *L. tarentula* (Moya-Laraño 1999; mass = 0.0007[carapace width + abdomen width]$^{2.63}$; $R^2 = 0.99$, $n = 190$, $P < 0.001$; based on laboratory measurements of all burrowing instars).

From 30 June to 21 July we established 30 replicates of each treatment, randomly assigning each pair to a treatment. Independence of replicates was ensured by choosing only spider pairs that were $>$10 m from other replicates. After being assigned to a treatment, each spider was visited once every night for a week and then once weekly. We recorded presence or absence of the spider in the burrow, feeding frequency, and prey type. In order to determine the potential prey value of each prey item, specimens of the observed prey were caught and weighed in the laboratory. Red foxes (*Vulpes vulpes*) prey on *L. tarentula* by digging out their burrows (Moya-Laraño 1999); thus, replicates that clearly had been destroyed by foxes were discarded from the analysis.

This design allowed testing the hypothesis of territorial exclusion, either by defense or cannibalism. If focal spiders in the TER treatment tend to disappear at a higher rate than focal spiders from the REF treatment, and the manipulations CONS and CONB had no effect on the rate of disappearance, we can conclude that interference takes place. In addition, if within TER the resident spider is the one more likely to remain in the area, we can conclude that *L. tarentula* females are excluding intruders by territorial interference. Furthermore, if the remaining spider (i.e., the winner) in TER shows a higher rate of mass gain than spiders in REF, we can infer that cannibalism often occurs during territorial defense. The above predictions were tested by nonorthogonal planned comparisons (Rosenthal and Rosnow 1985).

Experiment 2: behaviors during induced encounters outside the burrow

Encounters were induced at night during August. In order to ensure that the contest would take place within the potential territory and to minimize the effect of fighting over the burrow per se, which is itself an important resource (Fernández-Montraveta and Ortega 1990, 1991), only spiders that were active outside their burrows were used. Encounters were induced immediately after both contestants were found in the field with the help of a headlamp. The spider found first was designated the resident in the encounter, and a stone was placed in the mouth of her burrow to prevent her from entering the burrow during the experiment. The next animal that was found, the intruder, was placed in a vial and marked with enamel in order to distinguish her from the resident. The intruder was placed in an open 15 mm diameter opaque tube, and a plunger was used to slowly force the spider to exit the tube 5 cm in front of the resident spider. During our manipulations the resident spider was usually motionless or showed little movement. The interaction was considered as starting when the intruder was totally outside the tube and in front of the resident.

We recorded the behaviors of both spiders, the duration of the interaction, and the outcome. Forty-five interactions, using 90 different spiders, were induced during 15 consecutive nights. In order to determine if there was a behavior that could be assigned unequivocally to escalation, we categorized the different fighting behaviors. Behaviors were classified as (1) jump, one spider jumps suddenly towards the other; (2) contact, spiders make frontal contact; (3) retreat, one spider, considered the loser, runs away from the other; (4) pursuit, the winner chases the loser; (5) grapple, both spiders meet in close contact, with chelicerae close together and legs interlocked; (6) bite, one spider bites the other one or more times; (7) kill, a spider kills and subsequently eats the other. A contest was considered to have escalated if after a first contact, neither spider retreated and both spiders engaged in grapple behavior.

An interaction was over when one spider killed the other or when one spider ran away. If an interaction had not ended after 60 min, we stopped making observations. Once the interaction was over, we measured the carapace and abdomen of both spiders as well as the distance from the resident's burrow at which the interaction started.

Logistic regression (Hardy and Field 1998) was used to investigate the effect of percentage of the difference in size (PDS = [{carapace width of larger spider − carapace width of smaller spider}/carapace width of smaller spider]·100) on the probability of escalation, and was also employed to determine if hunger level and/or PDS influenced the probability of cannibalism. Hunger level of each spider was estimated by the residual of the regression of abdomen width on carapace width (Jakob et al. 1996). This latter variable is a reasonable measurement of hunger condition in spiders because it indicates how far a female is from her maximum fecundity potential (i.e., maximum number of eggs that she can lay; Legrand and Morse 2000, Kreiter and Wise 2001; J. Moya-Laraño, *unpublished data*).

RESULTS

Experiment 1: testing for territorial exclusion

Moving a focal spider to an artificial burrow closer to the resident increased by 7× the rate at which the focal spider abandoned her burrow (TER vs. REF, Fig. 1a; $G_1 = 18.83$, $P < 0.001$). Only one spider usually occupied the area at the end of the experiment (84% of the 19 replicates not attacked by foxes in TER). Both spiders disappeared in two replicates; in only one replicate were both spiders present at the end of the experiment. Size had no effect on which spider gained control of the territory, but residency status was important. The same proportion of bigger ($n = 8$) and smaller ($n = 8$) spiders eventually won the space ($G_1 = 0$, $P = 1$). The original resident won the space in 13 replicates, whereas intruders won the space only three times ($G_1 = 6.74$, $P = 0.009$). Locating the spider in a different burrow site did not affect the chances of the spider leaving the burrow more than locating her in an artificial burrow (CONS vs. CONB, Fig. 1a; $G_1 = 0.029$; $P = 0.863$). Locating the spider in an artificial burrow did not affect the chances of the spider leaving the burrow relative to spiders in natural burrows (CONB vs. REF, Fig. 1a; $G_1 = 0.164$, $P = 0.686$).

Eventual winners of space in the TER treatment gained mass at 2× the rate of spiders in REF (Fig. 2b; planned comparisons: TER vs. REF, $F_{1,60} = 9.91$, $P = 0.003$). Manipulations per se had no effect on mass gain (planned comparisons: CONS vs. CONB, $F_{1,60} = 0.09$, $P = 0.768$; CONB vs. REF, $F_{1,60} = 0.07$, $P = 0.796$). Cannibalism of the intruder by a resident in TER was directly observed twice.

The most common prey items (Isopoda and Tene-

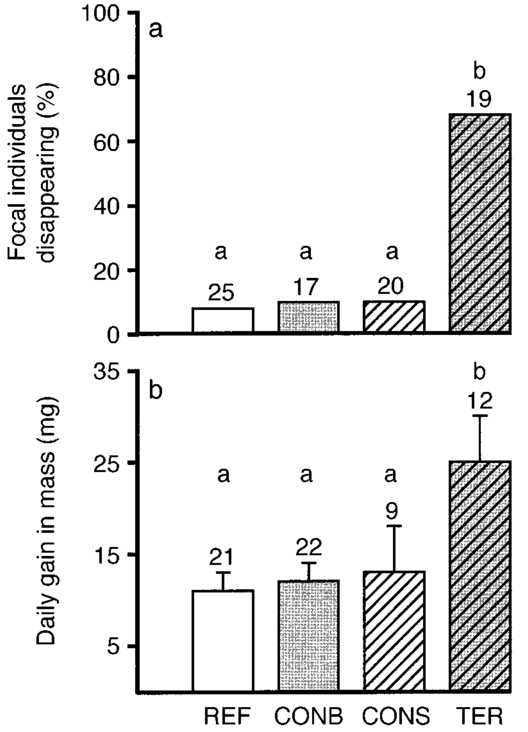

FIG. 1. Results of experiment 1. Sample sizes on the top of bars indicate the number of replicates that survived attacks by foxes. (a) ''Intruder'' spiders in the TER treatment disappeared from their burrows at a rate ~7× that of the other three treatments. (b) The rate of gain in mass (mean + 1 SE) by the winner in the TER treatment was double that of the focal spider in the REF treatment. The manipulations per se did not influence the rate of mass gain, as indicated by the similarity among REF, CONB, and CONS treatments. The letters above the sample sizes indicate treatments that are significantly different from each other.

TABLE 1. Relative contribution of each prey type to the diet of adult female *L. tarentula* (data obtained in 1435 visits to 210 females).

Prey type	Mean mass (g)†	No. observed being eaten
Male *L. tarentula*	1.43	4
Female *L. tarentula*	2.74	1
Isopoda	0.16	15
Tenebrionidae	0.10	34
Tettigonidae	1.68	2
Other		3
Unrecognizable		8

† Mass of male *L. tarentula*, Isopoda, and Tenebrionidae were obtained by weighing live individuals in the laboratory (sample sizes 24, 20, and 39, respectively). Female masses were obtained from the females in this study. The masses of Tettigonidae were obtained from species of similar size in the literature (Uvarov 1977).

brionidae) were one order of magnitude smaller than conspecific males and females (Table 1).

Experiment 2: behaviors during induced encounters outside the burrow

Escalation occurred in 71% (32/45) of the interactions. The smaller the PDS, the higher the probability of escalation (Fig. 2, logistic regression: beta = −0.07, $\chi^2_1 = 3.84$, $P = 0.050$). Resident spiders won more contests ($n = 29$) than did intruders ($n = 14$; $G_1 = 5.34$, $P = 0.021$).

Of the 32 encounters in which escalation occurred, 17 ended with ''grapple'' as the maximum level of escalation and 15 (i.e., approximately one-half of the escalations and one-third of the entire set of induced encounters) ended in cannibalism. Cannibalism was strongly dependent on escalation, as all cannibalistic encounters occurred only after escalation ($G_1 = 14.03$, $P < 0.001$). Within escalated encounters the probability of cannibalism was positively dependent on PDS (beta = 0.31; $\chi^2_1 = 8.16$, $P = 0.004$) and marginally negatively dependent on the body condition (inverse of hunger status) of the winning spider (beta = −0.92; $\chi^2_1 = 2.95$, $P = 0.086$). A model including the interaction term was not significantly different from the previous model (log-likelihood ratio test: $\chi^2_1 = 0.260$, $P = 0.610$).

DISCUSSION

Territoriality was demonstrated in *L. tarentula* females. Our results uncovered evidence for territorial exclusion mediated by defensive behaviors. In experiment 1 a single individual eventually occupied the space in most of the pairings in the TER treatment, with the resident usually winning the space. This residency asymmetry provides evidence of long-term de-

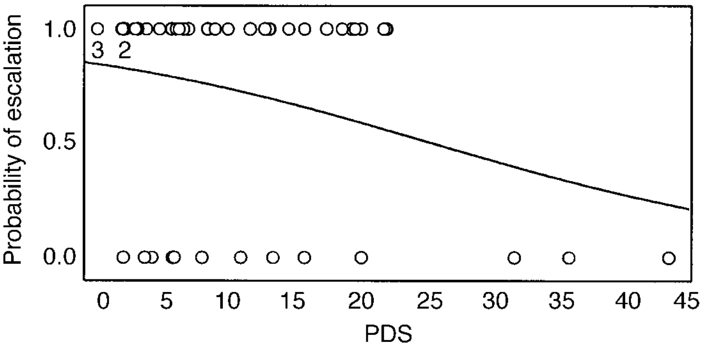

FIG. 2. The higher the PDS (percentage of the difference in size between contestants) the lower was the probability that a fight would escalate. Numbers under the points indicate overlapping points.

fense of a territory. Fights induced in experiment 2 exhibited escalation in over two-thirds of the cases, with resident spiders more likely to win the encounter. Because the most common prey are one order of magnitude smaller than female *L. tarentula* (Table 1), we can consider the observed behaviors as to be typical fighting rather than predation. The residence asymmetry has been further confirmed by the effect of asymmetries on contest duration (Moya-Laraño and Wise 2000). Escalation plus residency asymmetry in contest duration and outcome constitute evidence of defense during encounters. Thus, escalation occurred in experiment 2 and a resident advantage was confirmed by both experimental approaches, a pattern that establishes that *L. tarentula* adult females defend areas around their burrows.

Cannibalism occurred in one-third of the induced encounters in experiment 2, and its occurrence was indirectly inferred in experiment 1 from the higher rate of increase in mass of survivors in the treatment in which an intruder was placed in an occupied territory. One might argue that, rather than resulting from cannibalism, a higher rate of mass gain in TER could reflect the fact that in this treatment the winner spider reduces exploitative competition by excluding the losing spider. However, if that were true, spiders in CONS also should have increased their mass at a higher rate than in CONB, since in the CONS treatment a single spider also inhabited an area previously occupied by two spiders. Cannibalism among adult female *L. tarentula* occurred only after escalation, and escalation was most likely in encounters in which contestants were of similar size. Cannibalism as a predator–prey interaction is predicted to be both size- and hunger-dependent (Polis 1981, Dong and Polis 1992, Wagner and Wise 1996, 1997, Samu et al. 1999). However, cannibalism between *L. tarentula* females is not a conventional predator–prey interaction, because the outcome depends upon differences in size and hunger only after escalation of the interaction. If cannibalism between *L. tarentula* females were solely predation, the interaction would have been asymmetrical from the beginning, with the larger spider jumping, killing, and feeding on the smaller one.

Territoriality may have evolved in *L. tarentula* because excluding other spiders could increase the availability of insect prey and also improve access to males, which are both mates and a valuable food resource (Table 1; J. Moya-Laraño, J. Pascual, and D. H. Wise, *unpublished manuscript*). Cannibalism not only permanently excludes an invader from a territoriy, but is of direct benefit to the winner because female *L. tarentula* are food limited (Moya-Laraño et al. 1998, J. Moya-Laraño, J. M. Orta-Ocaña, J. A. Barrientos, C. Bach, and D. H. Wise, *unpublished manuscript*), and a conspecific is 10× more profitable as a prey than the most common prey items in the diet of *L. tarentula* (Table 1). Thus, in this species cannibalism may occur because the expected benefit of feeding on a conspecific outweighs the probability of being bitten and killed during the grappling stage. This benefit should be greater when the spider is hungry, and the probability of losing is lower when the spider is larger, which likely explains why hunger level and relative size influence the rate of cannibalism once a territorial encounter has escalated.

The territorial system of *L. tarentula* differs in several respects from that of another territorial spider, the funnel-web spider *Agelenopsis aperta* (Gerstch) (Riechert 1978*a, b,* 1979, 1981, 1982). First, in spite of the limited number of high-quality territories in desert grassland populations, adult female *A. aperta* rarely kill each other during fights. Either the inability of *L. tarentula* females to assess each other's intention during fights, or the fact that the lack of a territory is more costly for *L. tarentula* than for *A. aperta,* could explain the difference (Riechert 1982). Second, while the size of the territory in *A. aperta* females is genetically fixed, territory size in *L. tarentula* may decrease with resource availability, because female *L. tarentula* travel farther from the burrow when they are hungrier (Moya-Laraño et al. 1998, Moya-Laraño 1999).

Our field experiments with a natural, open population demonstrate that adult females of the Mediterranean tarantula exclude conspecifics from an area around their burrow. This territorial system is cannibalistic because cannibalism is a frequent consequence of escalation during territorial defense. Because it occurs in the context of agonistic interactions and is a consequence of escalation, cannibalism between adult female *L. tarentula* differs from conventional predator–prey interactions.

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