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OWNER-BIASED AGONISTIC BEHAVIOR IN FEMALE *LYCOSA TARENTULA FASCIIVENTRIS* (ARANEAE, LYCOSIDAE)

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Abstract. Matrices of the frequency of patterns of agonistic behavior of adult female *Lycosa tarentula fasciiventris* throughout intra-individual sequences were analyzed by means of an analysis of variance. Behavior differences were analyzed with regard to two factors: female size and previous occupation of the burrow. Results show that females use different tactics of agonistic behavior, depending on their previous occupation of the burrow, regardless of the relative size differences.

Resumen. Mediante un análisis de varianza aplicado a las matrices de frecuencia de las pautas en las secuencias intraindividuales de comportamiento agonístico, hemos analizado las diferencias en el comportamiento de las hembras adultas de *Lycosa tarentula fasciiventris* con respecto a dos variables: el tamaño y la ocupación previa del nido. Nuestros resultados indican que las hembras utilizan diferentes tácticas de comportamiento agonístico según su ocupación previa del nido, e independientemente de su tamaño relativo.

When studying agonistic behavior, the lack of intense aggression patterns has been explained by means of a theoretical game model of maximizing the consequences of behavior on fitness, given both the costs associated and the frequency of using that tactic among members of the population (Maynard Smith & Price 1973; Huntingford & Turner 1987). In contexts in which escalating a fight may be dangerous and information about the opponent is easily assessed, there may be different roles used to settle the contest (Maynard Smith & Parker 1976). These roles are determined by asymmetrical features between individuals, which may or may not be correlated with the individual winning ability or the relative resource-holding potential (Maynard Smith & Parker 1976; Hammerstein 1981). The expenditure of energy an individual makes is assumed to be adjusted to the value of winning the contest and the probability of doing it (Maynard Smith & Price 1973; Maynard Smith & Parker 1976).

Among spiders, several examples of biased agonistic behavior have been reported, especially among web-weaving species. Differences have been found to be usually related to individual size and previous residence (Buskirk 1975; Riechert 1978; Hodge 1987), although size difference may also affect the result in this latter case if greater than a critical value (Riechert 1978).

The agonistic behavior of adult females of the lycosid species *Lycosa tarentula fasciiventris* Dufour has been described from data obtained in our laboratory. During agonistic interactions, females show stereotyped patterns of behavior, and risk of bodily harm is relatively high. We think animals exchange information throughout these contests (Fernández-Montraveta & Ortega 1990) and, since escalation risk is high, this information can be expected to be accurate (Parker 1974). Animals will then be expected to accurately evaluate the contest and then use settlement strategies based on asymmetrical features of previous occupation of the burrow and size (Fernández-Montraveta & Ortega 1990). Since animals seem to occup their burrows for a long period and there is a relatively high investment of time and energy in burrow construction, individual behavior could be expected to differ with regard to residence, resident females displaying a higher interaction cost and persistence (Riechert 1988).

In this paper, interindividual differences in the frequency with which adult females of *L. t. fasciiventris* show patterns of agonistic behavior are measured with regard to the variables of size and previous occupation of the burrow. We attempt to verify if females of this species use different behavioral tactics, depending on these interindividual asymmetrical features.

METHODS

In this study 40 adult female *L. t. fasciiventris* were used. All the animals reached their adult instar in the laboratory and were maintained in isolation from the date of capture until observation. All the animals were from the same area, near the Universidad Autónoma, 15 km north of Madrid (Spain). Animals were weighed and measured after undergoing their last molt.

Observations were made in 30 × 15 × 15 cm terraria having a burrow constructed beside their front walls. The interior of the burrow was visible only during the observation time. Spiders were observed randomly paired with regard to their size, the intruder being moved to the observation terrarium just before the observation began. The resident female occupied the burrow inside the terrarium for at least 7 days before the observation date. Only females usually occupying the burrow, where they were fed, were taken into account. We made a total of 73 different pair observations, obtaining 34 interaction sequences. No animal was observed more than once a day.

Agonistic patterns of behavior were described (Fernández-Montraveta & Ortega 1990) from records of all the movements and activities of the animals during a minimum period of 30 min. Considering behavioral patterns as variables and individuals as cases, matrices were constructed in which the absolute frequencies (the number of times an individual exhibited a given behavioral pattern during the sequence) were represented. The absolute frequency matrices were transformed into relative frequency ones, representing the proportion between the display of each behavioral pattern and the total number of elements of the sequence. In order to carry out the analysis, an arc-sine transformation was applied to these resulting matrices.

Matrices were analyzed by means of a bifactorial analysis of variance, with the variables "previous occupation of the burrow" and "size" considered as the grouping factors. Two discrete levels were considered for each of these: "resident/intruder" for the former and "larger/smaller" for the latter. The analysis was applied by means of the program 7D, belonging to the BMDP87 package.

RESULTS

We analyzed 68 behavioral sequences from both the resident females and the intruders. Table 1 shows the results from the application of the analysis. There is no statistical interaction between the factors of "previous occupation of the burrow" and "size" for any of the analyzed behavior patterns (Table 1). There are significant differences in the mean frequency of all the behavioral patterns with regard to the factor of "previous residence," regardless of size. P-values are less than 0.05 in all cases, except for the "palpal drumming" pattern.

Figures 1 and 2 show the mean frequency of behavioral patterns for the variables of "previous occupation of the burrow" and "size". Intruder females more frequently use the patterns of "Motionless", "Approach" and "Go away" (Fig. 1). On the other hand, resident females more frequently use the patterns of "Foreleg Contact", "Pounce", "Foreleg Extension Chelicerae Spreading", ("Threat"), "Tangle" and "Cap-

Table 1.—F and P-values for differences in the mean frequencies of observed behavioral patterns relative to female size and previous residence (* indicates $P < 0.05$).

Pattern	Factor	F	P
Motionless	Residence	6.81	0.0114*
	Size	0.10	0.7531
	Interaction	0.08	0.7738
Approach	Residence	4.83	0.0317*
	Size	0.12	0.7358
	Interaction	1.35	0.2509
Go away	Residence	22.87	0.0000*
	Size	0.29	0.5936
	Interaction	0.01	0.9083
Contact	Residence	23.73	0.0000*
	Size	0.00	0.9882
	Interaction	2.88	0.0965
Pounce	Residence	36.39	0.0000*
	Size	1.02	0.3166
	Interaction	0.66	0.4221
Palpal drum	Residence	3.64	0.0641
	Size	0.58	0.4501
	Interaction	0.42	0.5199
Foreleg extension	Residence	49.33	0.0000*
	Size	0.01	0.9392
	Interaction	0.56	0.4567
Capture	Residence	18.55	0.0001*
	Size	0.00	0.9440
	Interaction	3.13	0.0832
Tangle	Residence	16.00	0.0002*
	Size	0.07	0.7934
	Interaction	1.15	0.2892

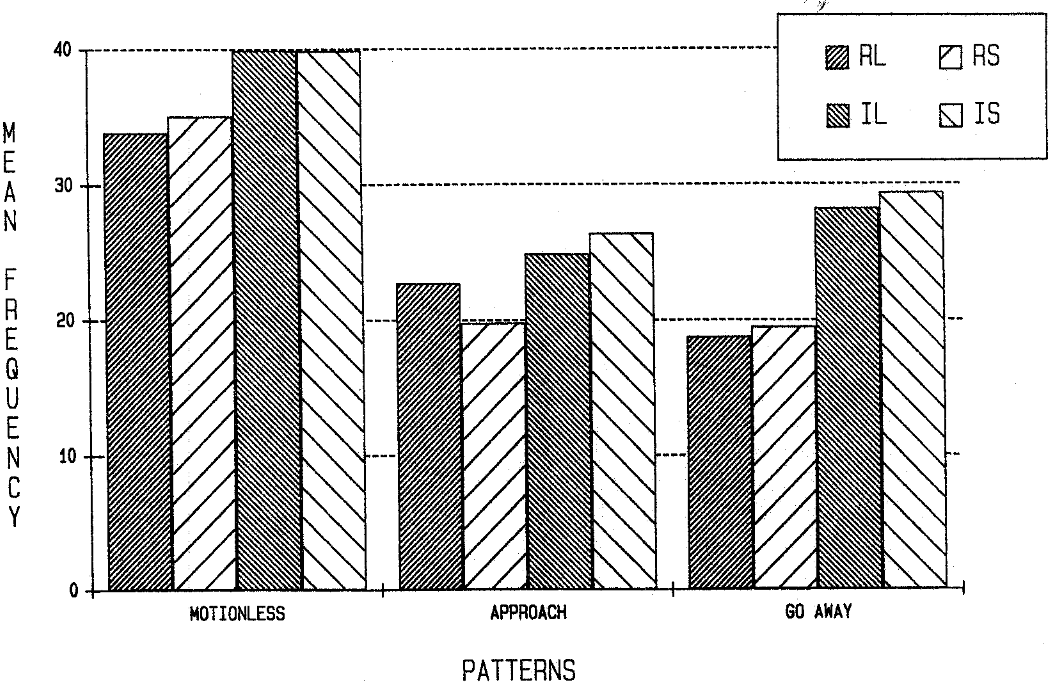

Figure 1.—Mean frequency of the behavior patterns more frequently shown by intruder females—"Motionless", "Approach" and "Go away"—with regard to relative size (S = smaller, L = larger) and previous occupation of the burrow (R = resident, I = intruder).

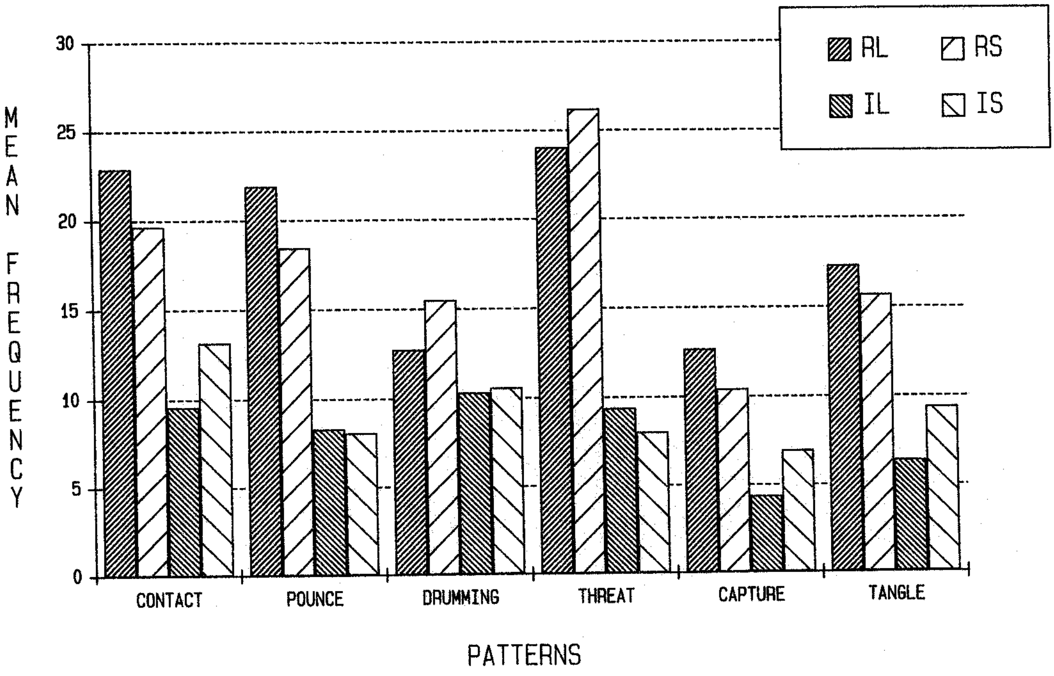

Figure 2.—Mean frequency of using the behavior patterns more frequently shown by resident females—"Contact", "Pounce", "Palpal drumming", "Foreleg extension and chelicerae spreading", ("Threat"), "Capture" and "Tangle"—with regard to relative size (S = smaller, L = larger) and previous occupation of the burrow (R = resident, I = intruder).

ture" (Fig. 2). Mean frequency of "Palpal Drumming" is also greater among this group, but is not significantly different (Table 1).

DISCUSSION

From our results, a high degree of intraspecific variability in the agonistic behavior of adult females of that spider species is obvious. When studying spider behavior, interspecific differences have been emphasized (Hollander et al. 1973; Stratton & Uetz 1983; Suwa 1984) and a lesser degree of attention has been paid to intraspecific variability (however, see Jackson 1986; Kronestedt 1986; Riechert 1988). Our results indicate that differences shown by females of *L. t. fasciiventris* in their agonistic behavior may be related to their previous occupation of the burrow but, in no case, to their relative size.

If we consider that behavior patterns are ordered according to their intensity—defined by the occurrence of contact (Glass & Huntingford 1988)—then behavior intensity seems to be greater for resident females than for the intruders in *L. t. fasciiventris* (Fig. 2). These latter tend to use to a greater extent those behavioral patterns of non-stereotyped approaching and retreating. Therefore, the behavior shown by resident females seems to be associated with a higher cost (Riechert 1988). These results can be interpreted as if adult females of this species were using the conditional strategy of "attack if resident and retreat if intruder" (Maynard Smith 1974) to settle the contests, regardless of their size difference.

Since size may be thought of as a factor influencing individual winning ability, and it is believed that animals exchange information about that factor (Parker 1974), it might be expected that spiders also adjust their behavior to their size differences. In our study, previous occupation of the burrow was not associated with greater physical ability since maintenance conditions were the same for all individuals, both those used as residents and those used as intruders. We think that the female agonistic tactic is based essentially on their previous residence, and that the effect of size difference is related to the interaction duration. This interpretation fits the inverse relationship we found between interaction duration and size differences in these kinds of encounters (Fernández-Montraveta & Ortega 1990).

We think, therefore, that our results fit the expectation that animals use an evaluator strategy to settle their agonistic interactions and exchange accurate information about relative ability to hold the resource. The factor of previously occupying the burrow apparently affects the assumption of behavior patterns with higher attack levels by resident females. This behavioral strategy should allow the contests to be readily settled for the resident female if size difference is not too small. Otherwise contest duration might be longer.

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