SPATIAL DISTRIBUTION OF *LYCOSA TARENTULA FASCIIVENTRIS* (ARANEAE, LYCOSIDAE) IN A POPULATION FROM CENTRAL SPAIN

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Abstract. The burrow spatial distribution pattern in a population of *Lycosa tarentula fasciiventris* from central Spain was studied. The developmental stage of the individual occupying the burrow, as well as the burrow spatial coordinates were measured during the spring and summer. A three-dimensional distribution pattern was obtained and Morisita, mean-crowding and variance-mean coefficient indices of burrow density were calculated. The burrow distribution pattern changed throughout the study period. Subadult burrow location shows a tendency toward instability whereas location stability of adult individuals is greater. In both cases there is a tendency towards clumping, which is lesser in the case of adult animals: if mean distances among burrows are compared between clumps, a tendency towards regularity results in the latter case. The observed distribution pattern might be a result of interspecific competition leading to a territorial system, with adult females constituting the structural support of the population.

Resumen. Hemos estudiado el patrón de distribución espacial de una población de *Lycosa tarentula fasciiventris* del centro de España. Durante la primavera y el verano, se midieron las coordenadas espaciales de los nidos, así como la fase de desarrollo del individuo que lo ocupaba. A partir de los datos, se ha reconstruido el patrón tridimensional de distribución, y se han calculado los índices de Morisita y mean-crowding, así como el cociente varianza-media de la densidad de los nidos. A lo largo del período de estudio se observa una modificación en el patrón de distribución de los nidos. Los nidos de los individuos subadultos muestran una tendencia a la inestabilidad, mientras que los ocupados por individuos adultos tienen una localización más estable. En ambos casos, se observa una tendencia a la agregación, que es menos marcada para los individuos adultos: si se comparan las distancias medias entre los nidos dentro de cada agregado, aparece una tendencia a la regularidad en el último caso. El patrón de distribución espacial podría ser el resultado de la competición intraespecífica, que determinaría un sistema de tipo territorial, siendo las hembras adultas el soporte estructural de la población.

In the non-social species, competition usually takes place in the form of struggling for a mate or for food (Burgess & Uetz 1982) and will be more severe between individuals of the same sex and age because they have similar requirements (McBride 1970; Dunbar 1986). This can lead to interindividual spacing that reflects resource distribution (McBride 1970). When resources are limited, competition is believed to be the main determinant for the population spatial structure (Riechert et al. 1973). Intraspecific aggression is a way of competition (Wilson 1975; Huntingford & Turner 1987), and species and/or individuals showing an active defense behavior may also be the ones showing the greatest regularity in their spacing patterns (Burgess & Uetz 1982).

Aggressive and defensive behavior has been reported in several spider families (Rovner 1968; Dijkstra 1969; Buskirk 1975; Riechert 1978; Jackson 1980; Jacques & Dill 1980; Goist 1982; Christenson 1984; Nossek & Rovner 1984; Hodge 1986, 1987; Wells 1988). Usually, studies of aggression as a means of competition have focused on male–male interactions in reproductive contexts (Rovner 1968; Dijkstra 1969; Jackson 1980; Goist 1982; Austad 1983). The study of competition for food or spatial resources not related to gaining access to a female received lesser at-

tention (Buskirk 1975; Riechert 1978, 1980; Hodge 1987). When competition for food resources was studied, spacing was shown to be actively maintained by means of agonistic interactions (Buskirk 1975; Hodge 1986) and to fit models ascribed to territorial systems (Buskirk 1975; Riechert 1978, 1982).

Most previous work on spatial distribution of spiders has been carried out on web-building species. The study of individual spatial distribution of species of Lycosidae, non-web-building ones, has not been too extensively put forward. Kuenzler (1958) reported that the spatial distribution of three species of the genus *Lycosa* showed a random pattern in a uniform environment. However, the active maintenance of spacing is a prevalent pattern (McBride 1970), and spiders seem more often to be territorial animals (Riechert 1980; Maynard Smith & Riechert 1984).

Our laboratory studies on the agonistic behavior of adult female *Lycosa tarentula fasciiventris,* suggest that agonistic interactions are a way of competing for burrows. Agonistic interactions usually occur inside the burrows, and the result of these interactions is the expulsion of one of the contenders (Fernández-Montraveta & Ortega 1990). Spiders of this species build tubular burrows in the ground, with an opening to the exterior which is sometimes surrounded by a cylindrical structure (Ortega 1986). Individuals spend most of their time in their burrows, and prey capture patterns seem to be related to them (Ortega 1985).

If the agonistic behavior of adult females of *Lycosa t. fasciiventris* is really a way of competing for burrow sites, it might be expected that individual spacing patterns fit a non-random distribution, probably a regular one (Burgess & Uetz 1982). That distribution would primarily involve individuals of the same age and sex. In this paper, we measure the burrow spatial distribution pattern in a population of *Lycosa t. fasciiventris* in central Spain in order to determine whether it fits the non-random distribution pattern predicted (Riechert 1980, 1982).

METHODS

We studied a population of *Lycosa t. fasciiventris* located in "El Goloso" ("Canal de Isabel II") near the Universidad Autónoma de Madrid. The study area was a rectangle 200 m long and 40 m wide, with its four boundaries artificially limited by a road and a three-sided metallic fence. This area is characterized by having a sandy substrate

with a poor water table and herbaceous vegetation. The site was visited daily between 0900 and 1400 h during the period from April to August 1984.

The study area was marked in a grid, covering the 200×40 m² rectangle. Along the 200 m axis, 1-m wide, parallel corridors were marked. These corridors were exhaustively covered in the successive visits, and the cartesian coordinates of the burrows occupied by *Lycosa t. fasciiventris* were recorded. Body measurements (prosoma length and width, as well as length of the first and the fourth leg pairs) and the developmental stage of each burrow occupant were recorded. Because it is difficult to accurately determine the developmental stage of the spiders, they were classified into three age categories: (1) subadult individuals born in 1983 (S-83), (2) subadult individuals born in 1982 (S-82) and reaching their adult instar in summer 1984, and (3) adult individuals. Immature individuals can be differentiated with regard to their year of birth, since they have markedly different sizes. With regard to sex, only adults and immature individuals at their penultimate instar can be differentiated. Animals were marked by means of a label attached to their prosoma.

A total of 131 burrows, only considering those occupied in at least two successive visits, were included in the total analysis. Since most of the molts were not recovered, we were unable to determine whether an unmarked occupant in a burrow was the same individual that was found previously. The chance that it was, according to its measurements, was used as a criterion.

Because the development rate of animals during the period studied is high, data were analyzed at two different times. First, data from May were taken into account. In this analysis, all the data were included. Secondly, data corresponding to July were analyzed. By that time, most of the initially marked S-83 individuals had disappeared, S-82 individuals had become adults and adult males usually did not occupy their burrows. Thus, only data from adult females were included in this second analysis.

The two sets of data were analyzed by introducing the coordinates of the burrows into a data matrix. With this matrix, a three-dimensional surface plot was obtained with the program Golden Graphic System (Golden Software, Inc.) in order to get a graphical representation of burrow density.

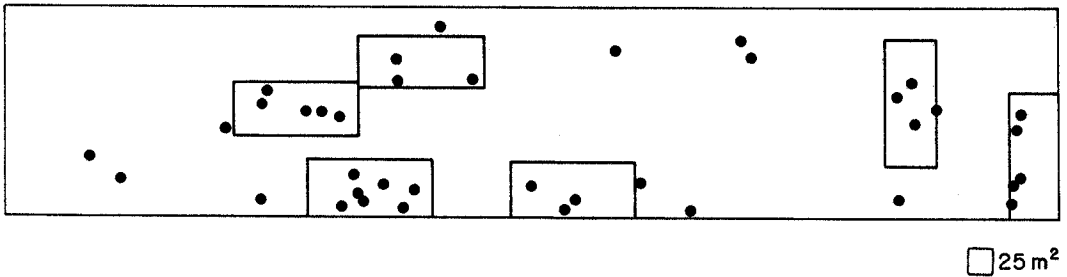Data corresponding to July were subjected to

□ 25 m²

Figure 1.—Study area plane with the location of the 38 adult female spider burrows which were included in the second analysis (July data). The six marked areas represent the rectangles of 250 m² superimposed on the aggregation patches.

additional analyses. These burrows were plotted as points on graph paper and counted using a sample lattice of 336 cells of 25 mm². The frequencies of burrows/cell were then calculated. The measures of aggregation we used were all based on the above frequencies. These measures were mean-crowding (Lloyd 1967), Morisita's index (Morisita 1959) and the variance-mean ratio (Pielou 1977). The first index provided information about the mean number of burrows per burrow co-occupying a cell, while the other two visualized the spatial pattern of the burrows. Significance of variance-mean coefficient was measured by means of

$$t = [(s^2/x) - 1]/(2/n - 1)^{1/2},$$
$$P < 0.05 \text{ (Kershaw 1973).}$$

After the coordinates of the burrows were graphically represented, several aggregation patches clearly different from one another became evident. Then a rectangle of 250 m² was superimposed on each patch, and only the burrows which fell into these rectangles were chosen for study (Fig. 1). The mean and the variance values of the distance from each burrow to its nearest neighbor were measured for each rectangle (Clark & Evans 1954). The mean distances were compared between rectangles applying a test of equality of means.

RESULTS

Table 1 shows the number of initially located burrows that continue to be occupied in the following visits with regard to individual age class. Data are from our first study phase.

The spatial distribution pattern of individuals in May is shown in Fig. 2. Figure 3 shows the spatial distribution pattern of individuals in July, including only adult females. When the two distributions (Figs. 2, 3) are compared, a change is

noticed in which the area of stronger aggregation in May disperses into several patches in which burrow density is high in July.

For the whole data corresponding to July, the variance-mean ratio (1.13) does not differ from random ($t = 0.590$). The Morisita's index (2.15) reveals that burrows are distributed with a certain tendency toward patching. Mean-crowding value (0.25), on the other hand, indicates the mean number of co-occupants to be relatively low. The mean distance to the nearest neighbor as calculated in each area (Table 2) shows some degree of spacing.

By comparing the mean distances to the nearest neighbor between the different patches, we found no significant differences among five of them. Only two of the patches differ from one another with regard to this parameter (Table 3).

DISCUSSION

A trend to burrow aggregation around certain areas is shown in both spring and summer but

Table 1.—Burrow location stability with regard to the developmental stage (age class) of the spider occupying the burrow. Individual location was more unstable during the early developmental stages than during the latter, and the entire number of animals was decreasing. There was a reduction of 60% in the population size. Disappearance of S-83 individuals accounts for 84% of this reduction. ([a] 34 of these individuals were found to reach their adult stage during the study period.)

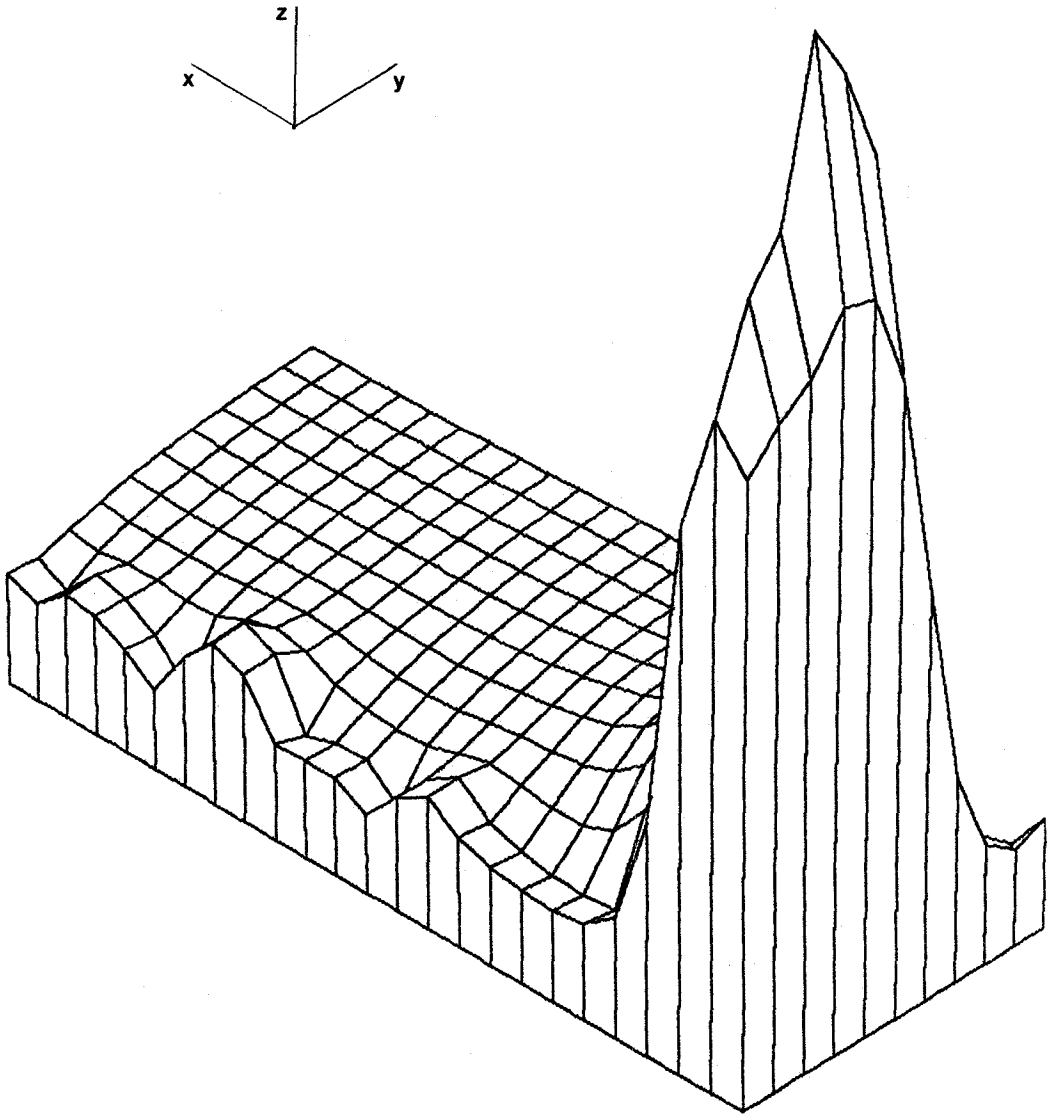| Age class		Numbers of burrows		
		Stable	Unstable	Total
Subadult	S-83	9 (12%)	66 (88%)	75
	S-82	37[a] (74%)	13 (26%)	50
Adult		6 (100%)	0	6
Totals		52 (40%)	79 (60%)	131

Figure 2.—Three-dimensional representation of burrow density distribution during the early study period (May). The axes labeled "x" and "y" represent the spatial coordinates of the area plane. The axis labeled "z" represents burrow density.

is stronger in spring. Spiders remain comparatively grouped during their early developmental stages (Fig. 2). A great instability of spatial location is also shown during these stages. Then, aggregation levels decrease, resulting in interindividual spacing together with a greater stability. These factors might result from increasing aggressive trends (Riechert 1978, 1980) and also from searching for suitable burrow locations, leading to the less clumped distribution pattern of adult individuals. At this point, interindivi-

dual distance, as well as location stability, are the greatest.

The spatial distribution of adult females might be considered as non-random. The existence of areas with differing density might reflect the heterogeneity of the study area conditions. In the small areas, the trend is for the females to be more regularly spaced out, suggesting spacing is actively maintained. Since adult female interactions occur in the laboratory resulting in one female eventually running out of the burrow
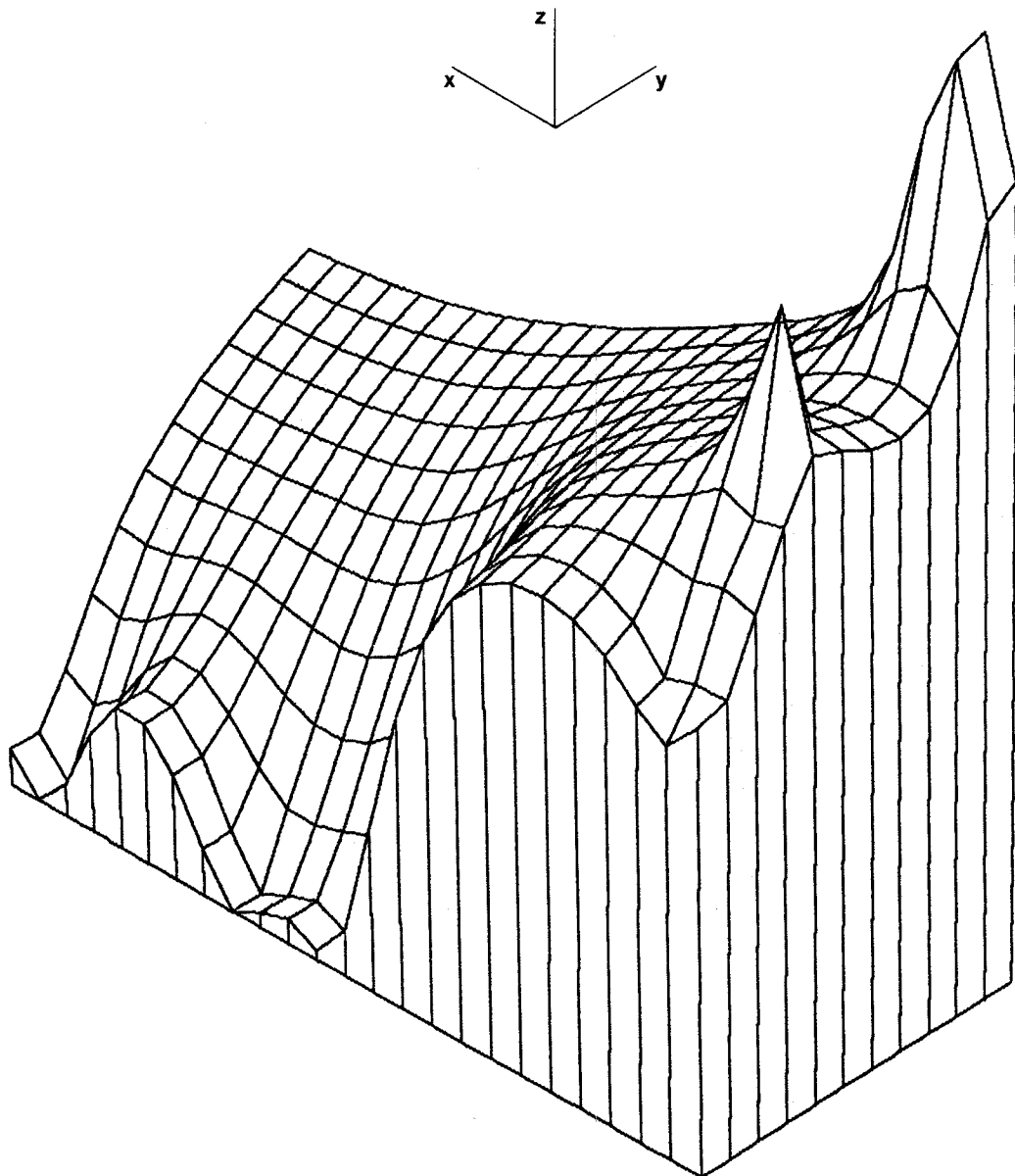
Figure 3.—Three dimensional representation of burrow density distribution during the latter study period (July). Axes labeled "x" and "y" represent the spatial coordinates of the area plane. Axis labeled "z" represents burrow density.

(Fernández-Montraveta & Ortega 1990), we might consider the distribution pattern to be a territorial system (McBride 1970; Riechert 1980; Huntingford & Turner 1987; Hammerstein & Riechert 1988). It might be an "overlapping territorial system" in which individuals defend an area around their burrow against intrusion, decreasing the attack intensity gradually as distance to the burrow increases (McBride 1970).

Data supporting the idea that spatial distribution of three Nearctic species of *Lycosa* was random (Kuenzler 1958) were based on individual location during their activity periods, not on the burrow location (two of the species not being burrowers). The burrow must be a significant resource as a shelter (Ortega 1986) as well as protection against extreme temperatures (Humphreys 1987; Riechert 1980). Moreover, it is

Table 2.—Mean values (meters) and SE of nearest neighbor distance in the studied subareas.

Areas	Mean	SE
1	1.20	0.34
2	0.56	0.13
3	0.50	0.04
4	0.66	0.18
5	0.57	0.07
6	0.45	0.19

Table 3.—P-value for comparisons between the nearest neighbor distance in the studied subareas.

| Areas | Areas | | | | | |
	1	2	3	4	5	6
1	—	0.09	0.003	0.250	0.097	0.1
2	—	—	0.650	0.660	0.932	0.65
3	—	—	—	0.207	0.436	0.65
4	—	—	—	—	0.630	0.47
5	—	—	—	—	—	0.57
6	—	—	—	—	—	—

probably associated with the predatory strategy of this non-web-building species (Burgess & Uetz 1982; Christenson 1984) and is not only a shelter to which animals return when disturbed (Kuenzler 1958).

The relatively great mean distance between the burrows may be a consequence of the spacing which results from agonistic interactions (Buskirk 1975; Hodge 1986; McBride 1970) and might reflect the minimal distance needed for intraspecific cannibalism to be reduced (Burger 1981). Territory size has been related to energy requirements and prey availability (Riechert 1978) and might be stabilized at its greatest value, which would correspond to extremely severe situations (Riechert 1980). Interindividual distances exceeding the web size have also been found in other species in which the web is considered to be the hunting territory (Buskirk 1975). Consequences of territorial behavior in Lycosa t. fasciiventris then would be that the individual's energy resources are probably assured. If territory size were fixed, it might set limits to the population size (Riechert 1980).

Because of their territorial distribution, adult females might through time be the structural support of the population. The size of the population studied shows sudden alterations that are probably due to dispersion and mortality during the individuals' early instars and, in the case of males, mortality during adult instar. In a population where females are competing for areas, whose size is based on available shelter and food supply, and where males are competing for females, the female spacing pattern may influence the distribution and size of the population to a greater extent than does that of other individuals in the population (Huntingford & Turner 1987).

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REFERENCES CITED

Austad, S. N. 1983. A game theoretical interpretation of male combat in the bowl and doily spider (Frontinella pyramitela). Anim. Behav., 31:59–73.

Burger, J. 1981. Super-territories, a comment. Amer. Nat., 118:578–580.

Burgess, J. W. & C. W. Uetz. 1982. Social spacing strategies in spiders. Pp. 317–322, In Spider Communication. Mechanisms and Ecological Significance (P. N. Witt & J. S. Rovner, eds.). Princeton Univ. Press, Princeton.

Buskirk, R. E. 1975. Aggressive display and orb defence in a colonial spider, Metabus gravidus. Anim. Behav., 23:560–567.

Christenson, T. E. 1984. Behaviour of colonial and solitary spiders of the Theriidae species Anelosimus eximius. Anim. Behav., 32:725–734.

Clark, P. J. & F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology, 35:445–453.

Dijkstra, H. 1969. Comparative research of the courtship behavior in the genus Pardosa. III: Agonistic behavior in Pardosa amentata. Bull. Mus. Nat. Hist. Nat., 2 sér., 41:91–97.

Dunbar, R. I. M. 1986. Aggression. Pp. 72–79, In The Collins Encyclopedia of Animal Behaviour (P. J. B. Slater, ed.). Collins, Oxford.

Fernández-Montraveta, C. & J. Ortega. 1990. El comportamiento agonistico de hembras adultas de Lycosa tarentula fasciiventris (Araneae, Lycosidae). J. Arachnol., 18:49–58.

Goist, K. C. 1982. Male-male competition in the orb weaving spider Nephila clavipes. Ph.D. Diss., Tulane Univ. Press, New Orleans.

Hammerstein, P. & S. E. Riechert. 1988. Payoffs and strategies in spider territorial contests: ESS-analyses of two ecotypes. Evol. Ecol., 2:115–138.

Hodge, M. 1986. The relationships between agonistic behavior and spatial organization in desert and tropical *Metepeira* spp. from Mexico. Amer. Arachnol., 34:5.

Hodge, M. 1987. Agonistic interactions between female bowl and doily spiders (Araneae, Linyphiidae): Owner biased outcomes. J. Arachnol., 15:241–247.

Humphreys, W. F. 1987. The thermal biology of the wolf spider *Lycosa tarentula* (Araneae, Lycosidae) in Northern Greece. Bull. British Arachnol. Soc., 7, 4:117–122.

Huntingford, F. & A. Turner. 1987. Animal Conflict. Chapman & Hall, London.

Jackson, R. R. 1980. The mating strategy of *Phidippus johnsoni*. III. Intermale aggression and a cost-benefit analysis. J. Arachnol., 8:241–250.

Jacques, A. M. & L. M. Dill. 1980. Zebra spiders use uncorrelated asymmetries to settle contests. Amer. Nat., 116:899–901.

Kershaw, K. A. 1973. Quantitative and Dynamic Plant Ecology, 2nd ed. Arnold, London.

Kuenzler, E. J. 1958. Niche relations of three species of lycosid spiders. Ecology, 39, 3:494–500.

Lloyd, M. 1967. Mean-crowding. J. Anim. Ecol., 36: 1–30.

Maynard Smith, J. & S. E. Riechert. 1984. A conflicting-tendency model of spider agonistic behaviour: Hybrid-pure population line comparisons. Anim. Behav., 32:564–578.

McBride, G. 1970. Theories of animal spacing: The role of flight, fight and social distance. Pp. 53–68, *In* The Social Use of Space in Animals and Man (A. H. Esser, ed.). Plenum Press, New York.

Morisita, M. 1959. Measuring the dispersion of individuals and analysis of the distributional patterns. Mem. Fac. Sci. Kyushu Univ., ser 2:215–235.

Nossek, M. & J. S. Rovner. 1984. Agonistic behavior in female wolf-spiders (Araneae, Lycosidae). J. Arachnol., 11:407–422.

Ortega, J. 1985. Qualitative and quantitative analysis of predatory behaviour of *Lycosa fasciiventris* Dufour (Araneae, Lycosidae). Biol. Behav., 10:55–65.

Ortega, J. 1986. Posibles relaciones entre el hábitat de *Lycosa fasciiventris* Dufour (Araneae, Lycosidae) y su comportamiento. Bol. R. Soc. Españ. Hist. Nat., 82, 1-4:121–129.

Pielou, E. C. 1977. Spatial patterns and their representation by discrete distributions. Pp. 113–165, *In* Mathematical Ecology. Wiley.

Riechert, S. E. 1978. Energy-based territoriality in populations of the desert spider *Agelenopsis aperta* (Gertsch). Symp. Zool. Soc. London, 42:211–222.

Riechert, S. E. 1980. The consequences of being territorial: Spiders, a case study. Amer. Nat., 117:871–892.

Riechert, S. E. 1982. Spider interaction strategies: Communication vs. coercion. Pp. 281–313, *In* Spider Communication: Mechanisms and Ecological Significance (P. N. Witt & J. S. Rovner, eds.). Princeton Univ. Press, Princeton.

Riechert, S. E., W. G. Reeder & T. A. Allen. 1973. Patterns of spider distribution (*Agelenopsis aperta* (Gertsch)) in desert grassland and recent lava bed habitats, South Central New Mexico. J. Anim. Ecol., 42:19–35.

Rovner, J. S. 1968. Territoriality in the sheet-web spider *Linyphia triangularis*. Z. Tierpsychol., 25: 232–242.

Wells, M. S. 1988. Effects of body size and resource value on fighting behaviour in a jumping spider. Anim. Behav., 36, 2:321–326.

Wilson, E. O. 1975. Sociobiology. Harvard Univ. Press, Cambridge.