ZEBRA SPIDERS MAY USE UNCORRELATED ASYMMETRIES TO SETTLE CONTESTS

Maynard Smith and Parker (1976) have shown theoretically that animal contests can be settled using uncorrelated asymmetries, i.e., asymmetries that make no difference to the pay-off to the contestants, and do not result from differences in their resource holding potential (RHP). For example, they argue that a contest could always be settled in favor of the "discoverer" of a resource (the resident), or the "latecomer" (the intruder), and that either convention would be an evolutionarily stable strategy (ESS).

Experimental data consistent with this hypothesis have been reported by Davies (1978) for the speckled wood butterfly and by Kummer (1971) for the hamadryas baboon. Maynard Smith (1974) suggested on the basis of a personal communication from M. F. Land that juvenile jumping spiders (species not given) also settle contests according to an uncorrelated asymmetry (the winner is the individual which advances first towards its opponent), but presented no data. The purpose of this communication is to provide evidence that the zebra spider, *Salticus scenicus* (Araneae: Salticidae), may use the uncorrelated asymmetry of arrival time to settle contests.

The zebra spider is a small jumping spider common throughout much of North America, Europe, North Africa, and Siberia. The species is 5.0–6.5 mm long and is easily recognized by three or four white bands on the dorsal surface of the abdomen. Males are slightly smaller than females and have large, black chelicerae. The spider is often seen on sunny and cloudy-bright days on the exterior walls of buildings, fence posts, and rock faces.

Female zebra spiders, collected in the field during July and August 1976, were observed at densities from $2.3/m^2$ to $5.4/m^2$ on an artificial wall (1.3 m $\times$ 2.7 m) erected in the laboratory. Each spider was individually marked on the abdomen with water soluble paint. Two spiders, selected at random, were observed for a 1-h period. Their locations were recorded once a minute along with the time and location of any contests (see below) with other spiders. Twenty-two 1-h observations were carried out with either unfed or satiated spiders, resulting in 44 spider-hours of observation.

Individual spiders were found to alternate between stationary and wandering modes. Prior to feeding, females spent an average of 54% of their time wandering; this increased to 70% once the spiders were satiated with *Drosophila* and ceased attacking them.

A total of 304 agonistic contests were observed. A contest occurred when two spiders oriented towards each other and both individuals spread their forelegs to the side or brought their palps together. One spider often retreated at this stage and the nonretreating spider was designated the "winner." Sometimes one spider continued to approach, and then one and sometimes both spiders raised their forelegs slightly. If neither individual retreated at this point, the forelegs were raised vertically above the body and the palps and chelicerae spread apart as the

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distance between the spiders continued to decrease. Few contests reached this stage of display, and only three resulted in physical contact. On the average, contests were broken off at about 5 cm, although in three contests the "loser" retreated at distances greater than 10 cm. Such behavioral patterns were never observed when the spiders approached prey. Thus the spiders do not mistake conspecifics for prey, but show true agonistic behavior.

The probability of "winning" an interaction depended on the behavioral mode of the spider at the time the interaction was initiated. Stationary spiders won 92.5% of their interactions (74/80), whereas wandering spiders won only 37.5% of theirs (84/224). This pattern was consistent for all spiders, regardless of the percentage of time they spent wandering. There is therefore no evidence that more aggressive individuals wander less. The wins of wandering spiders mostly came against other wandering spiders, a situation in which winning appeared to be determined at random. Feeding state had no effect on the increased probability of winning while stationary (92% pre-feeding; 94% satiated), nor did density.

Agonistic contests involving female spiders of the same size are much less frequent at the lower densities found in the field, but we have observed them often enough to believe that our laboratory observations are not artifacts.

Being stationary increases the probability of winning an interaction, because intruders are more likely to break off the interaction and retreat. Spiders, therefore, seem to have settled on the asymmetry of prior residence to decide contests. However, there seems to be no particular advantage to ownership of a small piece of wall. If there were a foraging advantage it would be expected that the majority of insects captured would be those that land within or walk into the defended area, yet this does not seem to be the case. Zebra spiders regularly stalk prey from distances exceeding 10 cm. Furthermore, as indicated above, satiation does not influence the probability of winning contests with intruders, as might be expected if the locations were being used as hunting sites by hungry spiders. (However, satiated spiders do spend more time wandering.) Finally, spiders remain in one spot only for very short periods at a time (less than 2 min in most cases in the field but averaging 6.2 min in the laboratory). Therefore the asymmetry used to settle contests appears to be uncorrelated in the sense of Maynard Smith and Parker (1976).

It is of considerable interest that in the majority of cases reported in the literature, it is the resident that has the advantage in the contest (i.e., the ESS settled upon is usually "intruder retreat"). One apparent example of the adoption of the "paradoxical" alternatives ESS ("resident retreat") has been reported in the social spider *Oecobius civitas* by Burgess (1976), but this strategy is uncommon, perhaps because of its vulnerability to "a mutant strategy in which the displaced owner retreats some way, then presents himself again in the guise of a newcomer" (Parker 1978, p. 851). In any event, truly uncorrelated asymmetries are probably rare in nature, as Dawkins (1976) suggests, and normally there may be some pay-off or RHP asymmetry in favor of the resident. This asymmetry may be minor and difficult to detect. Zebra spiders appear to demonstrate an uncorrelated asymmetry under laboratory conditions. However, in the field, some individuals seem to concentrate their wanderings to a restricted portion of the total

available space, suggesting some advantage of familiarity with an area. Further field research is needed on this point.

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