INTERSPECIFIC TOLERANCE IN SOCIAL
STEGODYPHUS SPIDERS (ERESIDAE, ARANEAE)

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ABSTRACT

The African social eresid spiders *Stegodyphus mimosarum* and *S. dumicola* exhibit extreme intra- as well as interspecific social tolerance. *S. mimosarum* individuals transferred over more than 20 km were accepted and immediately cooperated in strange conspecific colonies. In a laboratory experiment, adult females of both species formed mixed-species groups that spun and fed together.

INTRODUCTION

Among higher invertebrates social life has evolved in two taxa, in spiders and in insects. In spiders, social cooperation has arisen independently in several phylogenetic groups. The published schemes for the evolution of arachnid sociality suggest that two major forces may operate: a mutualistic cooperation among related or unrelated adults, and a prolongation of bonds between siblings (Buskirk 1981). The only arboreal genus in the cribellate family Eresidae, the Indo-African spider genus *Stegodyphus*, contains solitary as well as periodically and permanently social species, suggesting a pathway for evolution of sociality within this genus (Giltay 1927; Kullman 1972). Here we report on the social tolerance of two permanently social species, *Stegodyphus mimosarum* Pavesi and *S. dumicola* Pocock from Africa.

Both species inhabit dry thornbush country, living in colonies in compact, sponge-like silk nests found mostly in thorny trees. The animals mostly rest during daylight hours. The distribution of colonies is very patchy with several km between patches. New colonies are founded by groups of nearly, or fully, adult individuals emigrating from one colony to adjacent branches and trees. In addition, single adult females "balloon" by air, presumably founding new colonies far away (Wickler and Seibt 1986).

MATERIALS AND METHODS

We observed the animals in the field and the laboratory. Colonies were collected in 1985 from Swaziland, Transvaal and Natal (South Africa). They can easily be kept indoors for about a year. We fed them flies, small crickets and flour beetles.

Tolerance tests.—To test intraspecific tolerance in the field we, on three occasions, introduced individually marked *S. mimosarum* females into foreign colonies more than 20 km away. In addition, we removed several individuals from different colonies and combined them into new groups in the laboratory.

Interspecific tolerance was studied in·the laboratory. In order to avoid any bias from prior residence, we put five *S. mimosarum* and five *S. dumicola* adult females of similar size (6-7 mm in length; within a species, from the same colony) in an empty $10 \times 10 \times 10$ cm glass cube without any of their original nest material. Three such groups were started in parallel and observed for 55 days. We took 25 records of the spiders' local position and social aggregations for each of the three groups (never more than one per day). Records were taken at random day-times, the spiders were always quiescent and without food at that time.

RESULTS

Interspecific tolerance.—In neither case did we detect differences between the contacts with strange individuals and those between colony mates. One individual introduced into a foreign colony even joined some local individuals in subduing a prey insect within 5 min. There was no indication of colony membership identification. This result was the same as obtained in earlier experiments with the same species in Tanzania (Wickler 1973).

Interspecific tolerance.—Invariably, all 10 spiders (of both species) freshly introduced into a cage formed a dense clump within 1-3 hours and remained clumped for many hours. They started spinning within one hour and the combined effort produced a silken mass. When given food, members of both species joined to subdue and consume the prey. We did not observe interspecific aggression or avoidance. In fact, all feeding groups observed were heterospecific. These groupings on food were clearly induced by the feeding situation. Since each single spider might have been attracted by the food rather than by the other spiders, these feeding groups were eliminated from the following analysis which is based on 163 records of quiescent spider groupings. The animals were offered food about once a week; their immediate responses showed that they were hungry and, therefore, not tolerant just by satiation. Table 1 shows the frequencies of homo- and heterospecific groupings that occurred during the experiment.

All 10 individuals in a cage were clumped in 27 (= 31.4%) of the 86 heterospecific groupings, forming a dense ball with maximal bodily contact. This illustrates the strong thigmotactic tendency of these spiders. Although isolated spiders of either species would attempt maximal bodily contact with any substrate (thus coming to rest in corners, fissures of bark, etc.), other *Stegodyphus* individuals regardless of species are more attractive. This is an expression of the "interattraction" typical for social spiders (Darchen 1965).

Single spiders resting isolated from the other cagemates were recorded 58 times; in 45 cases it was a *S. dumicola*, in 13 cases a *S. mimosarum*. The difference is significant at $p < 0.01$ (binomial test) and may have resulted from *S. dumicola*'s higher locomotory activity.

Six or more individuals were found in 65 aggregations. These necessarily contained both species. In addition, 21 groups of less than six individuals contained members of both species (Table 1). Thus, heterospecific groups were

Table 1.—Frequencies of observed homo- and heterospecific groupings of *Stegodyphus dumicola* and *S. mimosarum* during 55 days.

Group size	Homospecific		Heterospecific
	S. dumicola	*S. mimosarum*	
1	45	13	
2	3	8	4
3	4	1	9
4	0	1	4
5	1	1	4
6			10
7			9
8			4
9			15
10			27

not a mere side effect caused by a tendency to congregate in larger groups (of more than five individuals). Groups of two to five individuals were heterospecific in 21 and homospecific in 19 cases (8 of *S. dumicola*, 11 of *S. mimosarum*), showing no apparent tendency of either species to aggregate separately.

The presence of *Stegodyphus* silk seems to attract individuals of either species. Searching individuals that come across a silk strand will follow it; texture and/or pheromones may be relevant cues. But two individuals, again regardless of species, coming from different directions on a completely clean surface, will contact each other in the typical manner without even touching the other's security thread.

DISCUSSION

In the field we observed intermigration between separate (presumably daughter-) colonies of both species over distances less than 10 m. Bradoo (1972) reports the same phenomenon for *S. sarasinorum* Karsch from India. To exclude familiarity between closely neighboring groups, we mixed individuals from far distant colonies. In all cases foreign individuals were tolerated in any conspecific colony. Kullmann (1968) and Bradoo (1980) obtained the same results for *S. sarasinorum*. Thus there seems to be no colony integrity in social *Stegodyphus* spiders.

Interspecific inter-colony tolerance has also been reported in the social spiders *Agelena consociata* Denis and *A. republicana* Darchen (Agelenidae), *Metabus gravidus* Cambridge (Araneidae), *Anelosimus eximus* Simon and *A. studiosus* Hentz (Theridiidae) and in *Mallos gregalis* Simon (Dictynidae) (Buskirk 1981), that is in all social species that have been so tested. Social spiders seem to differ from other social living animals in that they form open societies, in the sense that conspecific individuals are freely exchangeable between colonies.

All authors theorizing on sociality in spiders (and other animals, except mixed species bird flocks and fish schools) have understood 'social' as something restricted to conspecifics (Wilson 1971; Vehrencamp 1979; Buskirk 1981). Social *Stegodyphus* spiders are believed to recognize conspecifics (Bradoo 1980). However, Kullmann et al. (1971, 1972) mixed newly hatched young of the permanently social *S. sarasinorum* with those of the periodically or "condition-ally" (Millot and Bourgin 1942) social *S. lineatus* Latreille and kept this mixed

group for 3.5 months. This result is supported by the observation that young individuals of even solitary spiders allow contact with members of different species (Blanke 1972). The reactions of adult individuals therefore seemed more meaningful to investigate species recognition.

As the present study further shows, *Stegodyphus mimosarum* and *S. dumicola* colonies would be open even to members of the other species. The high degree of heterospecific groupings in the experimental situation indicates a considerable interspecific tolerance. Similarly, Krafft (1970, 1971) mixed the two social species *Agelena consociata* and *A. republicana* (for five days under observation) which suggests that species recognition might not be relevant in this situation. He did not mention the age class of his test animals, but all age classes co-occur in *Agelena* colonies, so interspecific tolerance may be present in adults.

Solitary spiders often live peacefully together as spiderlings and become cannibalistic later in their ontogeny. Neotenic retention of juvenile tolerance has therefore been assumed to be the first step toward communal behavior (Kullmann 1968; Buskirk 1981); it would not, however, account for interspecific tolerance. An interattraction of individuals could account for tolerance up to the point where competition would be counterselective. Under competition, selection (including kin-selection) can be expected to exclude xenogenetic individuals from tolerance. However, an individual's decision to attack or tolerate a stranger would still be governed by a cost/benefit ratio. For a socially living individual the cost factor may be most important: attacking will provoke defensive counteraggression, and the full risk of being severely damaged would fall upon the attacking individual, while costs arising from tolerance would be shared among all community members.

Mixed species *Stegodyphus* colonies are unknown from the field, perhaps because no one has looked for them. Both species co-occur closely in Transvaal, and the nearest interspecific colony distance that we encountered was 5 m within the same tree. On the other hand, our observations of the spiders suggest that the two *Stegodyphus* species would eventually separate according to their different behaviors (including walking speed, reaction times, etc.). *S. mimosarum* tends to live higher up in trees, while *S. dumicola* colonies are typically found closer to the ground (Seibt and Wickler 1988). Similarly in the genus *Agelena*, *A. consociata* prefers shadowy zones between lower bushes, while *A. republicana* builds its colonies in the crowns of trees exposed to the sun (Krafft 1970, 1971). Thus in both cases an ecological separation seems to counteract heterospecific groupings.

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Fig. 1.—Modified Malaise trap for capturing insects and spiders in spruce-fir forests, west-central Maine.

Choristoneura fumiferana (Clemens), the most destructive defoliator of conifers in the northeastern United States and Canada (Kucera and Orr 1981). Numerous insects and fewer spiders were captured in the Malaise traps; insect captures were summarized by Hilburn (1981). In this paper we describe the Malaise-trapped spiders, compare the trapped fauna with terrestrial- and arboreal-spider faunas of northeastern forests, and identify possible spider-Malaise trap interactions.

METHODS

Spiders were collected in 12 Malaise traps deployed at 12 sampling sites (1 trap/site) in spruce-fir forests of west-central Maine near Moosehead Lake. Three sites were in Somerset County; nine were in Piscataquis County. For details of sampling sites and sampling protocol, see Hilburn (1981) and Hilburn and Jennings (1988).

The Malaise traps were modifications of Townes' (1972) design and were placed on the ground in the herb-shrub layer (Fig. 1). Spiders and insects were captured in 1-pint (0.47-liter) jars containing 70% ethyl alcohol as a killing-preservative agent. Captured specimens were sorted and identified in the laboratory. Although there were six 48-h sampling periods for each site, collected spiders were combined from all sites and over all sampling dates (21 May to 29 June 1980).

Spiders were identified by the senior author; species determinations follow Kaston (1981) and other consulted sources including: Opell and Beatty (1976) for the Hahniidae; Leech (1972) for the Amaurobiidae; Chamberlin and Gertsch (1958) for the Dictynidae; Dondale and Redner (1982) for the Clubionidae; and Dondale and Redner (1978) for the Philodromidae and Thomisidae. Sexually