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HIGH PREY ABUNDANCE AND A REDUCTION IN CANNIBALISM: THE FIRST STEP TO SOCIALITY IN SPIDERS (ARACHNIDA)[1]

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ABSTRACT

Spiders of the species, *Achaearanea tepidariorum* (Araneae; Theridiidae), were held in enclosures under two prey regimes. One group of 100 spiders was provided with 100 fruit flies (Diptera; Drosophilidae; *Drosophila melanogaster*) per day and the second group of 100 spiders was provided with 1000 fruit flies per day. The number of spiders in enclosures dropped during the first six days in both groups. However, a higher rate of cannibalism in the low prey group caused the spider numbers in that enclosure to drop more rapidly than the high prey group. A greater proportion of the spiders in the low prey group settled into recognizable territories in the first six days than in the high prey group. Spiders in the high prey group tended to move more and therefore encounter conspecifics more frequently during observations. It is projected that tolerance, observed in these normally solitary spiders when large amounts of prey are present, could lead to more complex sociality if maintained under such conditions for an evolutionary period of time.

INTRODUCTION

Spatial patterns are a critical determinant of sociality in animals. If individuals rarely, or never, come in contact with conspecifics then it is difficult to imagine how sociality could evolve. Spiders are stereotyped as quick response predators that are frequently cannibalistic. Given those characteristics, one would expect that sociality would be extremely unlikely.

The spatial patterns displayed by many spider species appear to be strongly influenced by the distribution of prey (Burgess and Uetz 1982, Rypstra 1983). In species that maintain well-defined territories, those territories are small in populations living with high prey availability relative to populations living where prey are scarce (Riechert 1978, 1981, Uetz et al. 1982). In some natural populations of solitary spiders, aggregations have been observed in association with locally elevated insect abundances (Valerio and Herrero 1977, Honjo 1977, Burgess an Uetz 1982, Rypstra 1985). In enclosures the number of web-spiders that coexist is directly correlated with the amount of prey provided (Rypstra 1983). The fact that high prey levels can exert such control over the spatial

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patterns of solitary spiders makes it tempting to hypothesize that an abundance of prey is prerequisite to the evolution of sociality in some species (Buskirk 1981, Rypstra 1983, 1985).

The study reported here is an investigation of the behavior of a solitary spider maintained in high densities within enclosures with a large amount of insect prey available. In earlier experiments Rypstra (1983) found that intra-individual tolerance increased and cannibalism decreased in several spider species when maintained at extremely high prey levels in similar enclosures. Here, one of the species that appeared tolerant, *Achaearanea tepidariorum* (Araneae, Theridiidae), is observed more closely under two prey regimes. The goal of this study is to determine more specifically what happens during the first few days within enclosures as the spiders sort themselves out and an equilibrium density is attained. Various behavior patterns including aggressive interactions and cannibalism are quantified to gain a better understanding of how the high densities are maintained.

METHODS

Mature or pentultimate females of *Achaearanea tepidariorum* were collected around homes and buildings in the city of Hamilton, Butler Co., Ohio U.S.A. All spiders were between 4.5-5.0 mm in length. Prior to experimentation, individuals were held in six dram vials for 48 hours during which they were provided with water but no food. At the beginning of an experiment 100 spiders were released into an enclosure measuring 2.5 x 2 x 2 m. Laboratory-raised *Drosophila melanogaster* (Diptera, Drosophilidae) were released into these cages each day at 1100 h as prey for the spiders. In one enclosure 100 *Drosophila* were released and in the second 1000 *Drosophila* were released daily.

The animals were observed during a three-hour period (1300-1600 h) each afternoon for six days. At the end of each two-minute interval I recorded the number of spiders involved in various activities. Special attention was paid to the proportion of spiders participating in prey capture, feeding, spinning, and interactions with other spiders. After the observation period, I removed any prey remains and debris in the webbing and on the floor of the cage. It was possible to sort out the dead spiders from the dead *Drosophila*. In addition I was able to discern whether a particular item had been fed upon by the presence of silk wrapping and a characteristic shrunken appearance.

RESULTS

In both experimental groups the total number of spiders alive in the enclosures dropped during the six-day period (Fig. 1, Table 1). Significantly more spiders were lost in the low prey treatment than in the high prey treatment (Wilcoxon Paired Comparisons, $p < 0.05$) (Fig. 1, Table 1).

In both treatment groups about 13% of the spiders were involved in spinning or web maintenance during observation periods (Chi-squared Test, $p > 0.05$) (Table 2). However, more prey capture and feeding activity took place in the group provided with 1000 flies per day versus the group with 100 flies available (Chi-squared Test, $p < 0.05$) (Table 2).

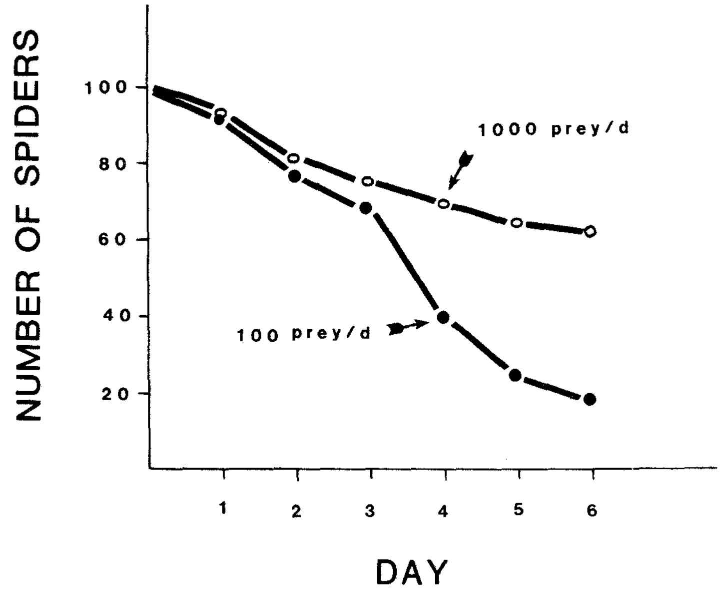

Fig. 1.—Total number of spiders living in enclosures maintained at two prey densities for six days.

I recovered close to 90% of the prey items over the course of the experiment (Table 1). In the group which had been provided 1000 flies/day, the number of flies that appeared consumed dropped during the six-days of the experiment (Kendall's Tau = -0.87, $p < 0.05$) (Table 1). In the other group the number consumed remained approximately the same over the whole period (Kendall's Tau = 0.20, $p > 0.05$) (Table 1). Of the spiders lost about 86% of them appeared to have been cannibalized in both groups which translates into a higher number

Table 1.—Numbers of *A. tepidariorum* and the prey they ate during a six-day period in which they were maintained in enclosures at either high prey (1000 fruit flies per day) or low prey (100 fruit flies per day) densities.

Day	Number of Living Spiders	Number in Territories	Number Spiders Cannibalized	Number of Prey Recovered	Number of Prey Fed Upon
Low Prey Group					
1	91	0	4	96	74
2	78	0	6	90	79
3	67	3	15	89	80
4	40	4	21	97	76
5	25	10	18	98	82
6	19	14	6	95	76
Cumulative Total	19	14	70	565	467
High Prey Group					
1	90	0	3	911	672
2	82	0	4	856	714
3	76	1	3	898	628
4	70	2	7	932	588
5	66	2	7	842	487
6	61	4	6	927	431
Cumulative Total	61	4	30	5366	3520

Table 2.—Percent of three hour observation times that spiders in enclosures were engaged in the activities of prey capture, feeding, web spinning and maintenance. All other behaviors including agonistic interactions, simple movement and holding still in web were lumped in the "other" category.

Day	Percent Time Spent Spinning		Percent Time Spent in Prey Capture[a]		Percent Time Spent Feeding[a]		Percent Time Spent in Other Activities[a]	
	low prey group	high prey group	low prey group	high prey group	low prey group	high prey group	low prey group	high prey group
1	12.8	13.7	25.6	32.5	15.7	28.2	45.9	25.6
2	19.2	15.8	20.1	33.1	18.9	44.7	41.8	6.4
3	14.2	14.5	19.8	34.8	17.3	39.2	48.7	11.5
4	10.2	12.1	20.2	38.1	31.8	38.8	37.8	11.0
5	13.2	12.5	28.4	37.8	34.2	43.1	24.2	6.6
6	11.1	11.7	26.2	36.1	30.1	35.2	32.6	17.0
Total	13.4	13.4	23.4	35.4	24.6	38.2	38.5	13.0

[a] A significant difference was found between low prey and high prey groups for these categories ($p < 0.05$).

cannibalized in the low prey treatment than in the high prey treatment (Wilcoxon, $p < 0.05$) (Table 1).

Spiders in both experimental groups interacted with one another regularly (Table 3). In a typical encounter one spider would orient toward the other with its first two pairs of legs extended and give the webbing one or two firm jerks. The approached spider usually reacted with a similar action. Interactions could intensify with a series of such exchanges for up to three minutes. Most interactions, however, ended after two to three exchanges spanning only a 40 to 80 sec time range (Table 3). Such bouts usually terminated with the retreat of one of the spiders. In the spider group maintained with 100 flies/day the aggressor was usually the one that retreated (Table 3). In the group maintained at 1000 flies/day, the recipient of the aggression was more likely to retreat (Table 3). In about 10% of all such encounters one spider actively chased the other away. Four observed aggressive bouts in the low prey experiment ended in cannibalism (Table 3). Only one bout ended in cannibalism in the high prey treatment group (Table 3). Significantly more interactions took place between conspecifics in the high prey experiment than in the low prey experiment (Wilcoxon, $p < 0.05$) (Table 3). Presumably a portion of this difference results from the greater number of individuals in one group. However, even if the number of interactions is standardized for the number of spiders present, each group has a distinct level of aggressive interactions (Wilcoxon, $p < 0.05$) (Figure 2). This difference is more pronounced after the third day of each experiment (Fig. 2). During more than 80% of the interactions a prey item was involved (Table 3). Several interactions in the high prey treatment ended with the fly abandoned by both spiders, whereas on only one occasion was a prey abandoned in the low prey treatment group (Table 3). Interchanges observed were slightly longer in duration in the low prey group than they were in the high prey group (Table 3).

As the days progressed more of the webs characteristic of this species appeared in the enclosures (Table 1). Although the enclosure into which the most prey were provided filled up with webbing more quickly than the other, the low prey enclosure contained more distinct webs than the other (Table 1). In addition, single individuals were observed occupying the webs in the low prey group for

Table 3.—Agonistic encounters between *A. tepidariorum* individuals in enclosures provided with low prey (100 fruit flies per day) and high prey (1000 fruit flies per day).

Parameter	Low Prey Group	High Prey Group
Number of Encounters Observed[a]	72	176
Number Encounters Involving Prey Item[a]	60 (83%)	141 (80%)
Number in Which Prey Item was Abandoned[b]	1 (1%)	3 (2%)
Number in Which Aggressor Retreated[a]	63 (88%)	60 (34%)
Number in Which Recipient Retreated[a]	12 (17%)	116 (67%)
Number ending in Cannibalism[b]	4 (6%)	1 (0.6%)
Mean Duration in seconds (range)[a]	58.4 (29.2-210.3)	41.5 (13.1-72.4)

[a] A significant difference was found between low prey and high prey groups for these categories ($p < 0.05$).

[b] There was insufficient data to test for a difference in these categories.

a two to three day span of time. Whereas spiders maintained in the high prey container moved in and out of spaces in the webbing approximately every 21 min, so that it was not possible to identify specific territorial boundaries.

DISCUSSION

These results further document an increase in tolerance for conspecifics displayed by the spider species, *Achaearanea tepidariorum*, at high prey densities that has been reported before (Rypstra 1983). This species reduces the amount of cannibalism, becomes non-territorial, and changes the nature of its interactions with conspecifics when plenty of food is provided. Under high prey conditions

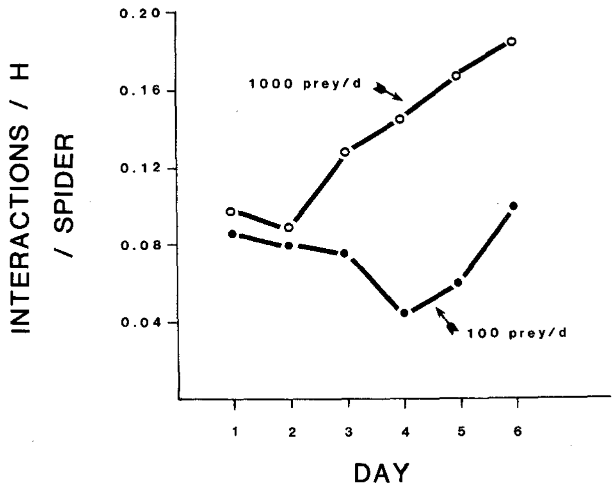

Fig. 2.—Number of aggressive interactions observed per spider per observation hour. Interactions took place among individuals maintained in enclosures at two prey densities for six days.

the behavior of this species becomes very similar to that of regularly social species that inhabit tropical regions (Buskirk 1981, Rypstra pers. obs.).

Prey abundance has been implicated in evolution of sociality in spiders in many cases. Aggregations of the orb-weaver, *Nephila clavipes* (Araneae, Araneidae), form around areas of high prey abundance in Peru (Rypstra 1985). Some species that build big web conglomerates do so to take advantage of high insect densities (Lubin 1973, 1974, Buskirk 1975, Rypstra 1979, Uetz et al. 1982). In addition there are numerous reports of solitary species in temperate regions clustered in areas where insects are abundant (Honjo 1977, Valerio and Herrero 1977, Burgess and Uetz 1982). These examples indicate that high prey abundance is important in the evolution of sociality via the parasocial route (sensu Wilson 1971). The alternative route to sociality in spiders involves an extension of the social tendencies frequently displayed by juveniles (Shear 1970, Buskirk 1981). Krafft et al. (1986) have been able to prolong the juvenile social period by providing the young with an abundance of food. Their experiments imply that food abundance could also be an important aspect in the evolution of sociality via this second pathway. Further evidence is provided by the geographical distribution of social spider species. All species are tropical or subtropical (Buskirk 1981), and live in areas characterized by consistently high insect abundances (Janzen 1973, Janzen and Pond 1975, Rypstra 1986).

One of the functions of territoriality is to insure access to resources (Brown 1964, Morse 1980). When food is super-abundant and resources are not limited, territorial behavior may break down. Carpenter and MacMillan (1976) developed a model permitting them to predict when nectar-feeding birds would shift from territorial to non-territorial states. The birds became non-territorial when resource availability was high in a manner similar to that displayed by the spiders in this study. When resources are super-abundant, no advantage is gained by defending a specific area that functions to guarantee access to those resources (Brown 1964).

In the high prey group the frequency of interactions between pairs of individuals is higher than in the low prey group (Fig. 2). Some part of the difference is due to the fact that fewer of these individuals settled into territories and more of them moved throughout the enclosure (Table 1). A similar difference has been observed in some studies of bird flocks. Pulliam et al. (1974) reported that individuals in flocks showed less aggression as conditions deteriorated. The birds accomplished this by reducing the number of encounters per individual and maintaining a defined inter-individual distance. This pattern is similar to what I observed the spiders doing in this experiment.

In part, the high frequency of interactions between conspecifics in the high prey treatment represents a stereotyped orientation response that they have to any vibration in their web. The number of fruit flies and the number of spiders moving throughout the intertwined webbing would naturally increase the number of times the spiders would have to orient and respond. The reduction in the intensity of the interactions is presumably because the spiders are not hungry and therefore are not driven to escalate the interactions. Some highly social cooperative spider species have a high rate of encounter interactions as they move through the webbing (Vollrath and Rohde-Arndt 1982, Rypstra pers. obs.), which operates as a form of communication network (Krafft 1982). With time these encounters which now appear aggressive could ameliorate into a more standard form of communication between individuals within a colony as sociality evolves.

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