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Evidence for Preadaption to Sociality in the Solitary Spider, Steatoda Triangulosa (Araneae, Theridiidae)

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Steven

1991

EVIDENCE FOR PREADAPTATION TO SOCIALITY IN THE SOLITARY SPIDER, *STEATODA TRIANGULOSA* (ARANEAE, THERIDIIDAE)

A Thesis
Presented to
the Faculty of the Department of Biology
Western Kentucky University
Bowling Green, Kentucky

In Partial Fulfillment of
the Requirements for the Degree
Master of Science

by
Steven Germishuizen
May, 1991

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EVIDENCE FOR PREADAPTATION TO SOCIALITY IN THE SOLITARY SPIDER, *STEATODA TRIANGULOSA* (ARANEAE, THERIDIIDAE)

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EVIDENCE FOR PREADAPTATION TO SOCIALITY IN THE SOLITARY SPIDER, *STEATODA TRIANGULOSA* (ARANEAE, THERIDIIDAE)

Steven Germishuizen May 1991 66 pages

Directed by: Rudolph Prins, Blaine Ferrell and Larry Gleason

Department of Biology Western Kentucky University

Steatoda triangulosa is a solitary domestic spider. In the laboratory, newly hatched *Steatoda triangulosa* spiderlings attacked and fed on prey organisms as a group. Kullman (1972) recognized three characteristics necessary to classify a spider as social: tolerance, interattraction and cooperation. Laboratory studies were conducted to test the hypothesis that *Steatoda triangulosa* may be preadapted to sociality according to these criteria. The group response was demonstrated by plotting the position of caged spiderlings in relation to a prey item before and after feeding. The intensity of the response was inversely proportional to the distance of the spiderlings from the prey. In studies to investigate cooperative feeding, spiderlings responded in greater numbers to larger prey. When presented with three similar-sized prey simultaneously, spiderlings responded significantly more often to one prey item than to more than one. To investigate tolerance, groups of spiderlings were kept for 21 days under different prey densities, and under conditions of high and low relative humidities. Cannibalism was inversely proportional to prey density. Increasing humidity decreased the incidence of cannibalism in groups of starved spiderlings.

CHAPTER 1

INTRODUCTION

The majority of spiders are solitary, aggregating only during early life and for mating (Shear 1970, Kullman 1972, Buskirk 1981). Spiders have strong tendencies towards aggressiveness and intolerance, which are extended even to conspecifics, and it would seem that these characteristics would be major barriers to the development of spider communities (Kullman 1972). It is therefore interesting to note that social phenomena beyond mating and juvenile aggregations have been reported from more than 33 spider genera in eleven families (Shear 1970, Buskirk 1981, Burgess, 1976). The anomaly of potential cannibals interacting socially makes the study of the evolution of sociality in spiders particularly fascinating.

Spiders show a range of social organization, from asocial species, which aggregate only during early life and for mating, to social species, which spend their lives in colonies that may contain several thousand individuals (Buskirk 1981, Riechert et al. 1986). Two families, the Theridiidae and Eresidae, are particularly rich with respect to diversity of social organization. For this reason, the behavior of representatives of these families have been extensively studied (Brach 1977, Fowler and Levi 1979, Christenson 1984, Nentwig 1985). These studies have proved valuable in the construction of proposed schemes outlining the evolutionary pathways from asocial to permanent social spiders such as those devised by Kullman (1972).

Definitions of sociality vary considerably depending on the group of organisms with which an investigator is most familiar. Thompson (1958) defined social behavior as, "a process of some kind occurring between individuals that has certain results involving more than one animal." Another definition equates sociality and intraspecific altruism: "Social (altruistic) behavior may be defined as the activity of an individual benefiting the young of another of the same species" (West 1967). While the former is too broad to be very useful, the latter insists on the condition of altruism, a qualification which might not always be apparent. Wilson (1971), the foremost insect sociobiologist, defined a society as "a group of individuals that belong to the same species and are organized in a cooperative manner." This definition, while being somewhat less restrictive than the others, requires a rigorous examination of the nature of cooperation, a subject which will be addressed later.

In order to identify spiders living in groups as possible social species, Burgess (1978) mentioned two criteria. These were: (a) the species must be found in statistically demonstrable clumps, and (b) individuals must exhibit some communication or interaction beyond that seen in male/female pairs. The reliance on these criteria depend on how communication is defined. The following is a broad definition that will be applied to this thesis: "Biological communication is the action on the part of one organism that alters the probability pattern of behavior in another organism in a fashion adaptive to either one or both of the participants." (Wilson 1975).

There are three characteristics required to categorize an organism as "truly" social and these provide a useful framework within which to view the evolution of sociality in arthropods. These traits are:

1) there is cooperative brood care;
2) there is reproductive division of labor, with more or less sterile

individuals working on behalf of fecund individuals;

3) there is an overlap of at least two generations in life stages capable of contributing to colony labor, resulting in offspring assisting parents during some period of their life.

Presocial is defined as the possession of two or less of these traits (Wilson 1971). Within the presocial category, Michener (1969a), identified several degrees of sociality for insects most of which have been widely used with respect to spider communities. These levels are:

1) Solitary - showing none of the three traits identified by Wilson (1971);
2) Subsocial - the adults care for their own offspring for some of the time;
3) Communal - members of the same generation use the same composite nest without cooperating in brood care;
4) Quasisocial - members of the same generation use the same composite nest and also cooperate in brood care;
5) Semisocial - as in quasisocial but there is reproductive division of labor; that is, where certain non-reproductive castes care for reproductive castes;
6) Eusocial - as in semisocial, but there is also an overlap in generations so that offspring assist parents.

While eusociality with reproductive division of labor has evolved several times independently within the insects (Wilson 1971), there is no evidence of this within the arachnids. This may be due in part to the absence of haplodiploidy, believed to be instrumental in the evolution of the extreme altruism found in the evolution of sterile castes, such as exhibited in the social insects (Trivers and Hare 1976). According to Wilson (1975), this remains one of the most important questions facing arachnologists.

There is considerable confusion in the literature concerning the terms widely used to describe levels of sociality. Buskirk (1981) defined semi-social as "members of the same generation using the same composite nest with *some* division of labor." [my italics], whereas Michener's (1969) definition, as reported by Wilson (1971), clearly stated that semisocial systems are characterized by *reproductive* division of labor. As Buskirk (1981) was summarizing from Wilson's (1971) work, it is not clear if this was a misinterpretation of Michener's (1969) original scheme, or if she was intentionally defining it thus. The two definitions are clearly different. As there is no evidence of reproductive division of labor within arachnids, it would be erroneous, according to Michener's (1969) scheme, to classify any spider systems that are presently understood as semisocial. However, there is some evidence, albeit inconclusive, of division of labor involving colony activities, in *Mallos gregalis* and *Agelena consociata* (Buskirk 1981). Buskirk's (1981) definition of semisocial organization might be applied to these social systems. For the purposes of this thesis, Michener's (1969) scheme will be strictly adhered to.

The term *parasocial* was introduced to include those presocial groups in which members of the same generation interact ie., communal, quasisocial and semisocial levels (Michener 1969). This term is useful when applied to spider systems because it can be used to describe one possible evolutionary route to true sociality, the parasocial route. Theoretically, this route involves the extension of mutualistic cooperation among unrelated adults promoted by favorable environmental conditions (Buskirk 1981). The parasocial evolutionary pathway would be from solitary, through communal to quasisocial. A second possibility could be the subsocial route, which operates when conditions are favorable to promote prolongation of the juvenile phase through maternal care. This would operate from the solitary level through subsocial to semisocial and is the scheme Kullman (1972) proposed for the Theriidiids and Eresids.

These suggested pathways should not be used as a general scheme for the evolutionary progression of social behavior among spiders, warned Buskirk (1981). She further stated that there are only two families, the Eresidae and the Theridiidae, for which the data suggest that evolution may have proceeded along these lines. In reality, elements from both routes may be in operation in single species simultaneously. The data for spiders in general suggests that social strategies have independently evolved along remarkably similar lines, in response to similar ecological pressures and in the presence of other behaviors (Burgess 1978). This challenges the researcher interested in the evolution of social spiders to explore the effects of environmental and social constraints on measurable criteria. Kullman (1972) provided three characteristics which need to be met in order to consider a spider as social, which are useful for these purposes. These are:

(1) Tolerance - Mutual aggressiveness must be abandoned for the time of the association. This feature requires intraspecific recognition so that the predatory response can be exclusively

directed at non-specifics.

(2) Interattraction - The cause of their association should not be restricted to the presence of abiotic factors. This implies an urge for association that requires intraspecific recognition.

(3) Cooperation - The members must show collective activities beyond their sexual behavior. These activities include: web construction and repair, capture of prey, communal feeding, individual brood care, and collective brood care.

Most of the behavioral studies have focused on species which show a relatively high degree of social organization such as *Anelosimus eximius* (Christenson 1984, Vollrath 1986) and *Anelosimus studiosus* (Brach 1977). Work with the solitary house spider *Achaearanea tepidariorum* provided useful, much needed insight on possible early evolutionary steps towards sociality from asocial ancestors (Rypstra 1986, 1989). Previous work has primarily focused on adult spiders, and little attention has been directed at the behavior of juveniles, particularly of solitary species. The premise of the present study is that insight into early evolutionary progression towards sociality within spiders can be gained by examining the behavior of juveniles of certain solitary species.

This study focuses on the behavior of early juvenile *Steatoda triangulosa,* a solitary Theridiid commonly found in human habitations throughout the United States (Comstock 1948). During the first few days after emerging from the egg case, the spiderlings cluster together on a finely woven communal web of their own construction. During this stage of their lives, I observed them attacking and feeding on prey in groups. Burgess (1978) reported that for most species, newly emergent spiderlings will aggregate and build a juvenile web upon which they attack prey as a group, but they never feed on the prey. It is not known whether group feeding, as observed in *S. triangulosa*, is common in species which are solitary as adults, but it is clear from the lack of such reports in the literature that this phenomenon has not been carefully studied.

In this thesis, the behaviors associated with the early aggregative phase are examined and related to their adaptive and evolutionary significance in terms of the development of sociality with the following objectives:

1) To gather background natural history information, through field and laboratory observations, necessary in comprehending the experimental work which follows.
2) To conduct experiments with juvenile *S. triangulosa* in which the effects of prey abundance and relative humidity upon the three criteria necessary for sociality, namely, tolerance interattraction and cooperation (Kullman 1972) are investigated.
3) To forward the hypothesis that *S. triangulosa* possesses some important preadaptations to a permanent social mode of existence in addition to certain characteristics that preclude the formation of a society. Furthermore, to discuss the evolutionary pathway that may have been followed.

CHAPTER 2

NATURAL HISTORY

INTRODUCTION

Members of the genus *Steatoda* build characteristic webs, consisting of a loosely woven platform with a series of vertical strands extending down from the sheet (Comstock 1948, Kaston 1972). Some of the strands may contain viscid silk, which allows crawling prey items to stick to them for long enough for the spider to attack and wrap the prey in silk. After the prey is wrapped it is taken to the upper portions of the web where it is fed on. The wrapping behavior is characteristic of the Theridiids, and is made possible by the comb-like structures found on the tarsi of the fourth pair of legs. Silk is hooked on the combs and flung over the prey. This can be performed without coming into contact with the prey and may reduce the risk of the spider being injured by the struggling prey. In this way, Theridiids are able to catch prey much larger than themselves (Comstock 1948).

There are no published studies on the life cycle or ecology of *S. triangulosa*, or any closely related species to supply the necessary information to place the experimental data which follow in ecological context. Notes kept May 15, 1989, until April 5, 1990, of observations made in three basements which served as collecting and study sites for the duration of the study, provided the following general picture of the natural history of *S. triangulosa*.

From October until February no spiders were found. Adult and sub-adult females were first observed in late February. By the middle of March, the first egg cases were found in the webs of females. The egg cases were white, spherical, and loosely woven and the eggs could easily be seen through them. Females typically remained in the same webs during their entire breeding cycle and continued to lay eggs at approximately weekly intervals for two months or more. Juveniles usually molted once while in the egg case and then emerged as second instars. These juveniles were about one millimeter long, and looked and behaved similarly to adults. They dispersed after a few days on the juvenile web. Second and third instar juveniles were found on tiny finely woven webs in cracks in the walls and floor. Red mites or juvenile isopods were commonly found in their webs. Females left all the empty egg cases in their webs, so the webs contained a legacy of the occupant's reproductive efforts for the previous year. Unoccupied webs contained an average of 12 egg cases (8-17, n=12). By late September, no new egg cases could be found and by the fourteenth of October no adult females were evident. It is not known where they went.

At one study site, the only prey found in webs were isopods and centipedes, which apparently comprised the majority of the spiders' diets. At this site, spider webs virtually lined the walls of the basement with most of them occupied by *S. triangulosa* or *A. tepidariorum*. Underneath the webs lay a mat of isopod and centipede exoskeletons about two centimeters deep. At another study site centipedes and flies appeared to comprise most of their diet.

To supply further life history information, studies were conducted to determine:

1) the average length of the juvenile phase at a natural study site and in the laboratory;

2) the fecundity of *S. triangulosa* - specifically, how may eggs per egg case were laid, and approximately how many egg cases were produced by each female during a season;

3) if there were any interactions, such as maternal feeding, between the mother and the juveniles during the juvenile phase;

4) the time between egg laying and juvenile emergence from the egg case;

5) if juveniles fed while on the juvenile web in their natural environment and in the laboratory, and if juveniles feeding on the communal web delayed their dispersal.

METHODS

A field study to determine the average length of the juvenile phase was carried out from July 9 to August 1, 1990, in one of the study sites. This was a large basement containing very high densities of *S.triangulosa*. Fourteen *S. triangulosa* webs, all of which contained females that had at least one egg case, were marked. These webs were built between the bottom angles of the wall and floor, or on a ledge about one meter above the floor. Every day for 20 days the webs were examined at 1800 h for newly emergent spiderlings. The date that they emerged and the date on which the last spiderling had left the web were recorded.

To determine if the time taken to disperse in the field would be the same under laboratory conditions, a gravid female that had not yet laid eggs was placed in a 30 cm^3 cage, which contained a cloth screen with two millimeter mesh on two sides. This size mesh allowed juveniles through, but not adults. The cage was placed in the laboratory where the temperature averaged 24.5 C (22 C - 26 C) and the average relative humidity was 52.5% (46% - 65%). The photoperoidic schedule was LD 16:8. After the female had built a web she was fed an *ad libitum* diet of mealworms (*Tenebrio molitor*). For each egg case she laid the dates when the egg case was completed, all the spiderlings emerged and the last juveniles had dispersed were recorded. Whenever juveniles were present on the web, daily observations were made to determine if there were any interactions between the mother and the juveniles.

In order to determine if, by feeding groups of juveniles on the communal web, the rate of dispersal could be decreased, a gravid female was placed in a cage similar to the one used in the previous study. Each group of juveniles that emerged was fed one or two *Tribolium confusum* larvae every day for nine days. The number of spiderlings feeding on the prey were recorded, the activity of the mother observed, and the number of juveniles remaining on the web each day recorded.

In order to determine the average number of eggs per egg case at the field sites, eggs were removed and counted from 43 egg cases collected from all three study sites.

RESULTS

Once the spiderlings emerged, they built a juvenile web supported on the main strands of the mother's web. This web was of much finer silk and much more closely woven than the mother's, although basically of the same structure. From the 14 marked webs there were 10 occasions on which juveniles emerged during the period of the study. An average of 21.5 (18 - 25) young emerged from the egg cases. Young remained on the web for an average of 1.9 (1-3) days. In two instances juveniles remained on the web for longer than five days. In one case it was not known when the juveniles emerged, but six juveniles were observed on the web for five consecutive days. These appeared to have distended abdomens and may have fed while on the juvenile web, although they were not observed feeding. On another occasion, five third instar juveniles were observed clustered on the web for five days before dispersing. Their exuviae stuck to the web, indicating that they had molted on the web.

The mother was never observed contacting young or responding to their movements. She usually remained on the web the entire time, except on one occasion when she disappeared at the same time as the juveniles dispersed.

From the gravid adult female kept in the laboratory, the following information was gathered:

1) The juveniles spent one to three days on a finely woven juvenile web which they constructed on the female's web, before dispersing.
2) Eleven egg cases were laid between July 13 and September 26, after which she stopped laying (Laboratory-reared females laid 10 - 15 egg cases throughout the two years I have kept them in the laboratory). Forty three egg cases taken from the field and laboratory contained 16 - 67 eggs (mean = 38).

3) No interactions such as maternal feeding were observed between the mother and the juveniles.

4) There was a period of seven to nine days between the laying of each egg case. The period of time between the laying of the egg case and the juveniles emergence from the egg case was 24 - 27 days.

The results from feeding juveniles on the communal web in the laboratory are summarized in Table 1. Of 27 spiderlings that originally emerged from the egg case, six were still on web after eight days. After the eighth day the emergence of the juveniles of another egg case made it impossible to tell which spiderlings were from the first egg case, so no more data could be gathered. During these observations, the mother did not interfere with the spiderlings. Young occasionally wandered onto the mother's web, but they received little or no response from the mother. On one occasion, the prey got stuck on part of the mother's web, and a group of spiderlings attacked it. The mother moved toward the prey, but stopped short and did not attack. There was only one case of sibling cannibalism during the experiment.

Table 1. Numbers of juvenile *Steatoda triangulosa* found on the communal web, the number of *Tribolium confusum* larvae provided and the number juveniles observed feeding each day.

Day	Number of prey items provided	Number of juveniles feeding		Number of juveniles on web
1	2	#1 - 6	#2 - 3	27
2	1	#1 - 4		24
3	2	#1 - 4	#2 - ?	15
4	1	#1 - 3		13
5	2	#1 - 3	#2 - 1	7
6	2	?		8
7	0			6
8	2	?		6
9	New juveniles emerged			

#1 - indicates the first prey item introduced

#2 - indicates the second prey item introduced

DISCUSSION AND CONCLUSIONS

In the laboratory, on an *ad libitum* diet, *S. triangulosa* females laid an average of 11 spherical, loosely woven egg cases, at intervals of seven to nine days during one breeding season. This is similar to the number of egg cases laid at the field study site. Buskirk (1981) identified a trend in which the number of eggs per egg case is inversely proportional to the degree of social organization of a species. For example, the solitary *Acheaearanea tepidariorum* has been reported to lay egg cases containing a mean of 223 eggs (Valerio 1977), while the quasisocial spiders *Anelosimus eximius* and *Anelosimus studiosus* lay egg cases with approximately 36 eggs (Christenson 1984, Brach 1977). Based solely on this relationship, one would expect *S. triangulosa* to be a social species. Buskirk (1981) does not include the number of egg cases that are laid during the breeding life of each species in her analysis; therefore the number of eggs per egg case may not be a precise indication of fecundity. However, based on observations and literature reports, I suspect that this trend would also be apparent when considering total number of eggs. It might be concluded that the decrease in fecundity is compensated by the increased survival of young, due to benefits such as maternal care, resulting from social existence. This would make the social species K-selected, relative to solitary species. However, the reason for the relative K-selection of *S. triangulosa* may have little to do with social organization, but rather due to precocial development. For example, *S. triangulosa* juveniles are considerably larger (0.28 mg) than *A. tepidariorum* juveniles (0.016 mg) (Valerio 1977) when they emerge from the egg case, and are able to individually attack and feed on prey 11 times their own weight (Refer to page 45). Attempts to feed both individual and grouped second instar *A. tepidariorum* were not successful. Newly hatched juveniles did not attempt to attack even relatively small prey. The ability of *S. triangulosa* to catch larger prey would make a greater range of prey available ensuring an increased survival of young.

Juvenile development took 24-27 days from laying to emergence from the egg cases in the laboratory at an average temperature of 24.5 C and an average relative humidity of 52.5%. Juveniles typically molted once while in the egg case. After emerging from the egg case, unfed juveniles spent one to three days on the juvenile web. The mothers usually remained on the same web for the entire period of the study and they did not appear to interact with their offspring. In the natural environment it appeared that juveniles occasionally fed while on the juvenile web and this may have delayed their dispersal. When juveniles were fed on the juvenile web in the laboratory, they did not disperse as rapidly as unfed groups. Krafft, et. al. (1986) found that in the maternal-social spider *Coelotes terrestris* under-fed colonies dispersed significantly earlier than did *ad-libitum*-fed colonies. The authors suggested that the behavioral mechanism related to dispersal of young, while not clearly known, might involve a fading of interattraction, or an increase in agonistic behavior induced by food competition.

CHAPTER 3

GROUP RESPONSE TO PREY

INTRODUCTION

The literature contains reports of juvenile aggregations of essentially asocial spiders attacking prey as a group, but these reports are purely descriptive and somewhat vague. For example, Burgess (1976) reported that while spiderlings in their early tolerant phase may attack and wrap prey as a group, they never feed.

When *T. confusum* beetles were introduced into the juvenile webs of laboratory-reared *S. triangulosa* it appeared that most of the spiderlings responded quickly by congregating around the prey. While not all the spiderlings would contact the prey, most of them would move in the direction of the prey. Spiderlings that were closer to the prey seemed to take a more direct route towards the prey, while those further away seemed to move more randomly.

This experiment was conducted to test whether a group of juvenile *Steatoda traingulosa* respond by moving closer to prey introduced to the juvenile web and whether this response decreases as the distance between the spiderlings and the prey increases. The significance of this is discussed in relation to the web as an effective mass communication medium, strongly favoring social organization.

METHODS AND MATERIALS

Adult, gravid *S. triangulosa* females were collected from the study sites during February and March, 1990. They were brought into the laboratory and housed in glass cages where they usually built a web in a day or two. The environmental conditions in the laboratory were the same as reported in Chapter 3. Spiders were fed *ad libitum* on fruit flies *Drosophila melanogaster* and mealworms.

The cages were checked periodically for egg cases. Major developmental stages could easily be distinguished. Spiderlings emerged from the chorion and molted once while still in the egg case. Eggs cases containing spiderlings that were still enclosed in the chorion were white, once they had emerged from the chorion they became slightly yellow, and after the first molt they were brown. Once the spiderlings had emerged from the chorion the egg cases were removed from the mother's web and placed in petri dishes. It usually took one to two days from when the first spider emerged, to when they were all out of the egg case. The same day that all the spiderlings were free of the egg cases, they were placed into experimental cages. Each experimental cage was a cube with a volume of 1000 cm^3 and was constructed of plexiglass. Twenty spiderlings were placed in each of the cages. Eight cages were set up as replicates, as soon as the spiderlings became available for use. Each cage contained the offspring of a different mother and spiderlings from each of the locations were represented, but not in equal numbers because eggs had to be used when they became available.

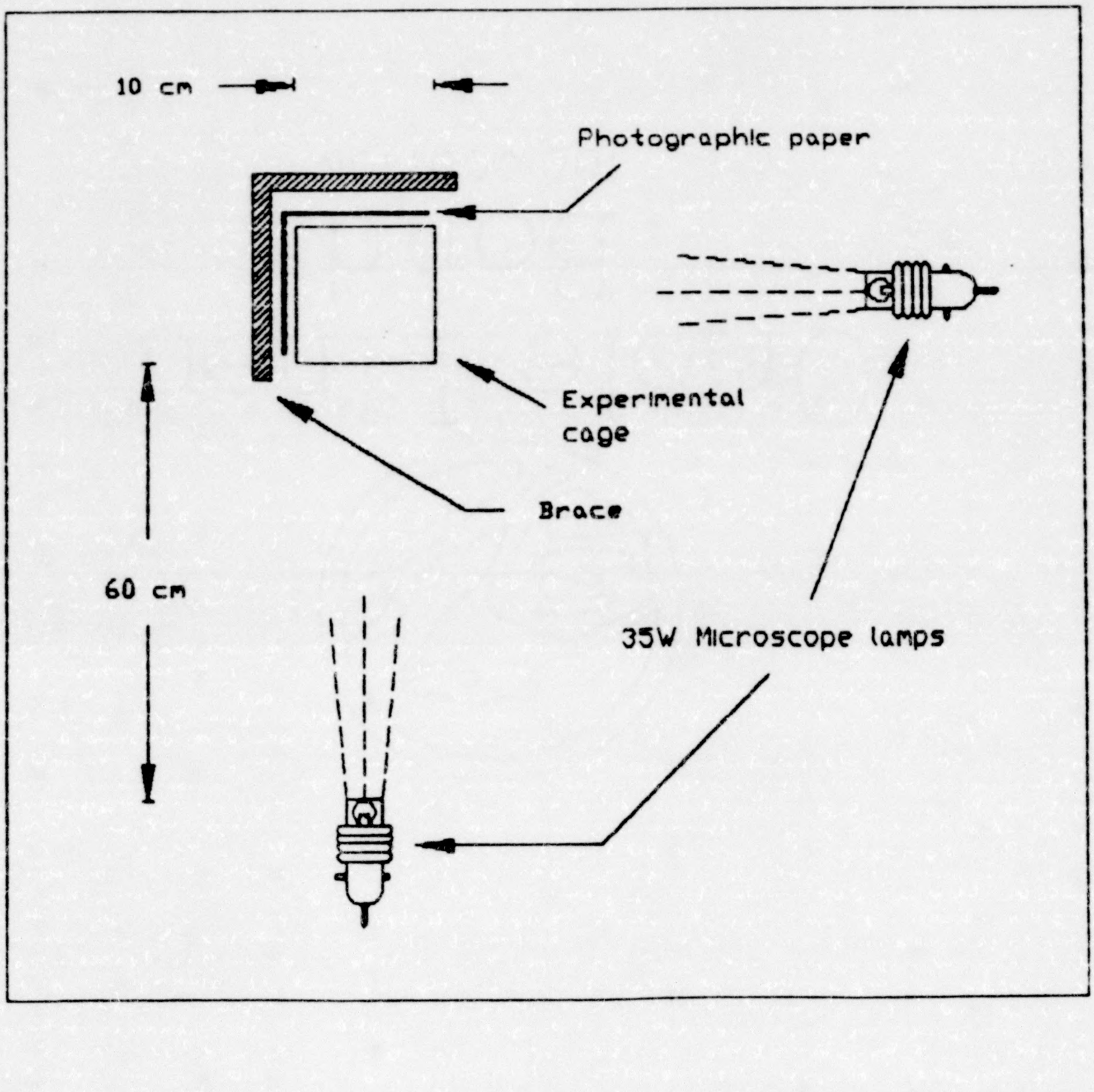
The experiments were conducted from May 9 to May 21, 1990. Each cage was left for three days after the spiders were introduced, during which time the spiderlings built a communal web. The positions of each of the spiders in their cages was then determined as follows: A single cage was positioned between two 35 watt microscope lamps placed 60 cm away from the cage at 90 degrees to one another (Fig. 1). Extreme care was taken when moving the cages so as not to disturb the spiderlings. The main lights in the laboratory were turned off and a photographic safe light was switched on. Two pieces of photographic paper were secured behind the cage as illustrated in Figure 1. The lamps were flashed for a period of 0.5 to 1 second, recording images of the spiderlings' shadows on the photographic paper. There seemed to be no behavioral changes induced by this alteration in the the light. Spiderlings always remained motionless during the entire process. Two shadowgrams were produced for each cage over which a grid of 1 cm squares was placed. By analyzing the photographic images, the X, Y and Z coordinates were determined for each spiderling.

A single *T. confusum* adult was then dropped into the cage where it usually became ensnared in the web. Occasionally the cage had to be gently inverted to allow beetle that had wriggled free and fallen to the bottom of the cage to fall back into the web. Spiders usually responded by moving rapidly towards the prey within the first minute after introduction of the prey. Their positions were recorded again three times during the period five to ten minutes after feeding. The X, Y and Z coordinates for each spiderling and the positions of the prey were loaded into a computer program that makes use of the pythagorian principle in the following formula (Uetz and Cangialosi 1986).

$$\text{Distance } (1,2) = [(X_2 - X_1)^2 + (Y_2 - Y_1)^2 + (Z_1 - Z_1)]^{1/2}$$

From this formula, the computer calculated the distances of each spiderling from the prey for each set of coordinates. For the 'before feeding' groups, the position of the prey was taken to be the position at which the prey first became ensnared after feeding. This never varied from the prey position five minutes after feeding, so prey position for before feeding was taken from the first shadowgram. The groups were observed for one hour after the data were recorded and notes made concerning the activities of the spiderlings around the prey site. The distances of the spiderlings from the prey before feeding were compared with the distances 10 minutes after feeding. The most intense response was usually observed within 10 minutes after feeding. The distances for each treatment were ranked and the means of the 'before feeding' and 'after feeding' ranks were calculated. The ranked data were compared for significance using the Wilcoxon signed rank test. A regression analysis of distance from prey against order of distance from prey, before feeding and 10 minutes after feeding was conducted, and the slopes were tested for significant differences using a covariate analysis which measures the extent to which regression slopes are different.

Figure 1. Diagramatic representation of the equipment used to record the positions of the spiderlings in experimental cages.


10 cm
Photographic paper
Experimental cage
Brace
60 cm
35W Microscope lamps

RESULTS

The mean distances of the spiderlings from the position of the prey before- and 10 minutes after- feeding are presented in Table 2. Spiderlings were significantly closer to the prey after feeding ($P = 0.004$, Wilcoxon signed rank test). Figure 2 is a plot of the mean distances of the spiderlings from the prey before and after feeding, against order of distances from the prey. Spiderlings that were nearer where the prey first landed moved a greater distance in the direction of the prey after the prey was introduced. Regression analysis of the lines for Before feeding ($r = 0.61$) and After feeding ($r = 0.69$) indicated that the lines were highly significantly linear ($P < 0.01$). A treatment by covariate interaction which measures the extent to which regression slopes are different, indicated that the slopes were highly significantly different ($F = 0.073$, $P > 0.99$). This test works on the assumption of homogeneity of regression slopes, so a non-significant F indicates that the slopes are different.

Figures 3 and 4 are diagrams of typical experimental cages with the distribution of spiderlings before feeding and 10 minutes after feeding respectively. The spiderlings, shown as circular icons, have a clumped distribution on the juvenile web. By shining a microscope lamp into the cage one could discern the shape of the web. The positions of the spiders before feeding conformed closely to the general shape of the densest portions of the juvenile web, although some web strands could be seen filling most of the cage. Spiderlings could therefore have access to virtually any part of the cage, but always showed the clumped distribution illustrated in Figure 3.

Figure 4 shows a typical distribution for spiderlings 10 minutes after feeding. The prey which is represented by the black diamond has 15 of the spiderlings congregated around it in a two centimeter radius.

DISCUSSION AND CONCLUSIONS

It is widely acknowledged that web building spiders use vibrational signals transmitted through the medium of the web as their primary source of information (Barth 1982, Tietjen 1986). Initiation of prey capture in particular depends upon vibrational cues (Barth 1982). There is some conjecture about the possible role of air-borne vibrations as a communicatory stimulus. Walcott (1963) found that the metatarsal lyriform organ of *Achaearanea tepidariorum* is highly sensitive, and can derive more information from air-borne sound than it can from vibrations through its web. However, there is no indication from behavioral observations and physiological experiments as to how they make use of this information. The roles of other sensory stimuli such as chemicals and visual cues are recognized as important in web building spiders (Krafft 1982), particularly for courtship. Work by Kullman (1972) on the quasisocial spider *Stegodyphis sarasinorum,* showed that the spider will attack and bite a vibrating paraffin ball. This confirms the overriding dependence that web building spiders have on vibratory cues, particularly for prey location. It is most likely that the spiderlings in my experiment were responding primarily to the vibrations in the web, caused by the movement of the prey item caught in the web.

Table 2. Distances of *Steatoda triangulosa* spiderlings from prey immediately before- and 10 minutes after- feeding with *Tribolium confusum* adults.

		Distance from Prey			
		Before feeding		After feeding	
Order of Distance from Prey	n	Mean	SE	Mean	SE
1	6	0.97	0.21	0.00	0.00
2	6	1.65	0.28	0.00	0.00
3	6	2.02	0.54	0.67	0.21
4	6	2.45	0.66	1.50	0.66
5	6	2.78	0.73	2.10	0.51
6	6	3.23	0.68	2.62	0.76
7	6	3.42	0.70	2.88	0.84
8	6	3.73	0.71	3.10	0.78
9	6	4.23	0.68	3.93	0.75
10	6	4.68	0.81	4.53	0.84
11	6	5.47	0.96	4.91	0.82
12	6	5.65	0.99	5.45	0.95
13	6	6.40	0.85	6.25	1.20
14	6	6.64	0.91	6.40	1.17
15	5	6.80	0.83	6.82	1.15
16	5	7.50	0.30	7.38	0.99
17	5	7.95	0.12	7.55	0.17
18	4	8.48	0.16	8.33	0.23

ANOVA- $P < 0.001$ ($F = 21.6$, d.f., 1,17)

Significant differences between ranked data for the 'before' and 'after' feeding is $P = 0.004$ (Wilcoxon signed rank test)

Figure 2. Mean distance from prey before and after juvenile *Steatoda triangulosa* responded, in order of distance from prey.

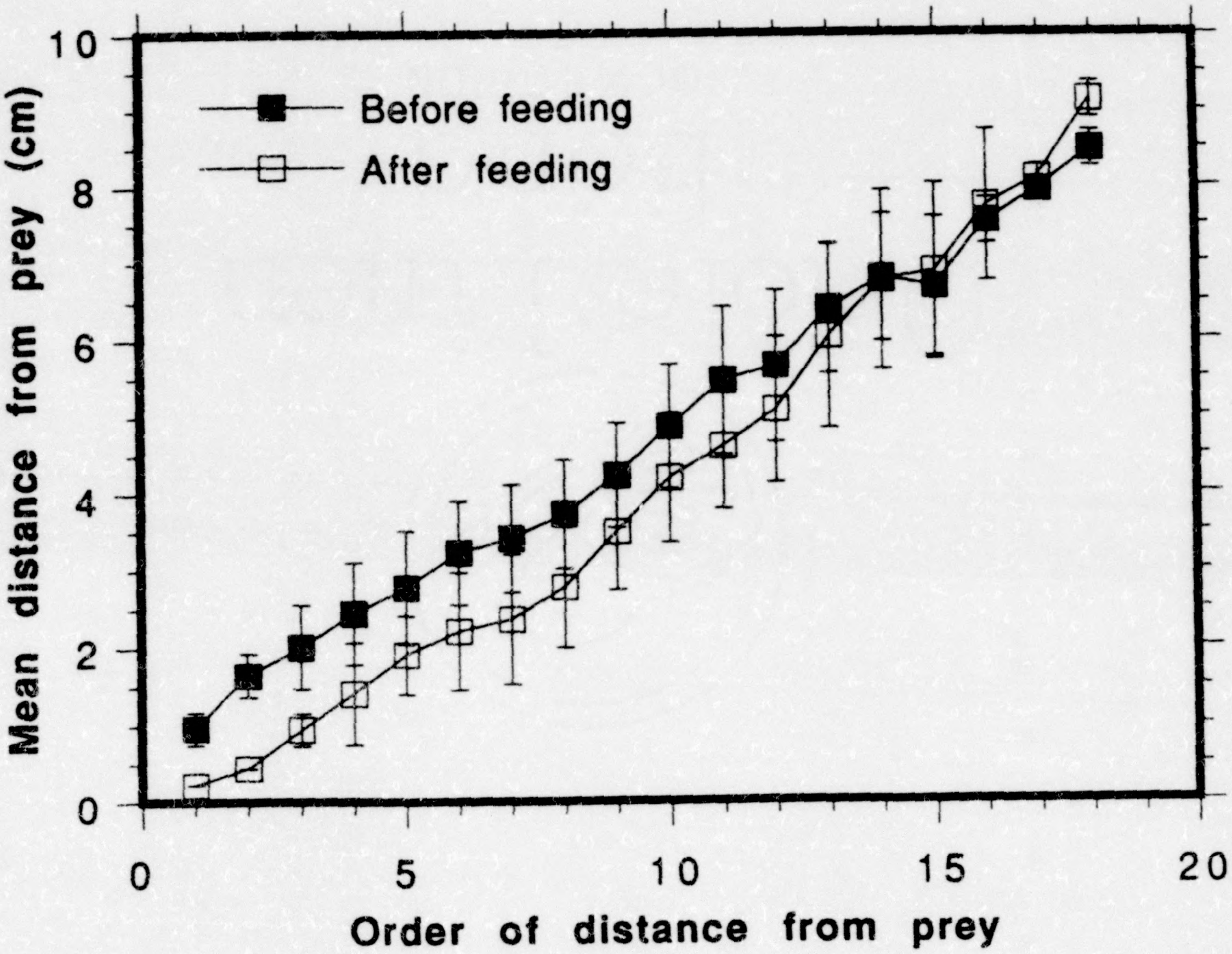

Before feeding
After feeding
Mean distance from prey (cm)
Order of distance from prey
0
2
4
6
8
10
0
5
10
15
20

Figure 3. Typical experimental cage before feeding with *Tribolium confusum* beetles. Juvenile *Steatoda triangulosa* are represented by the dangling icons.

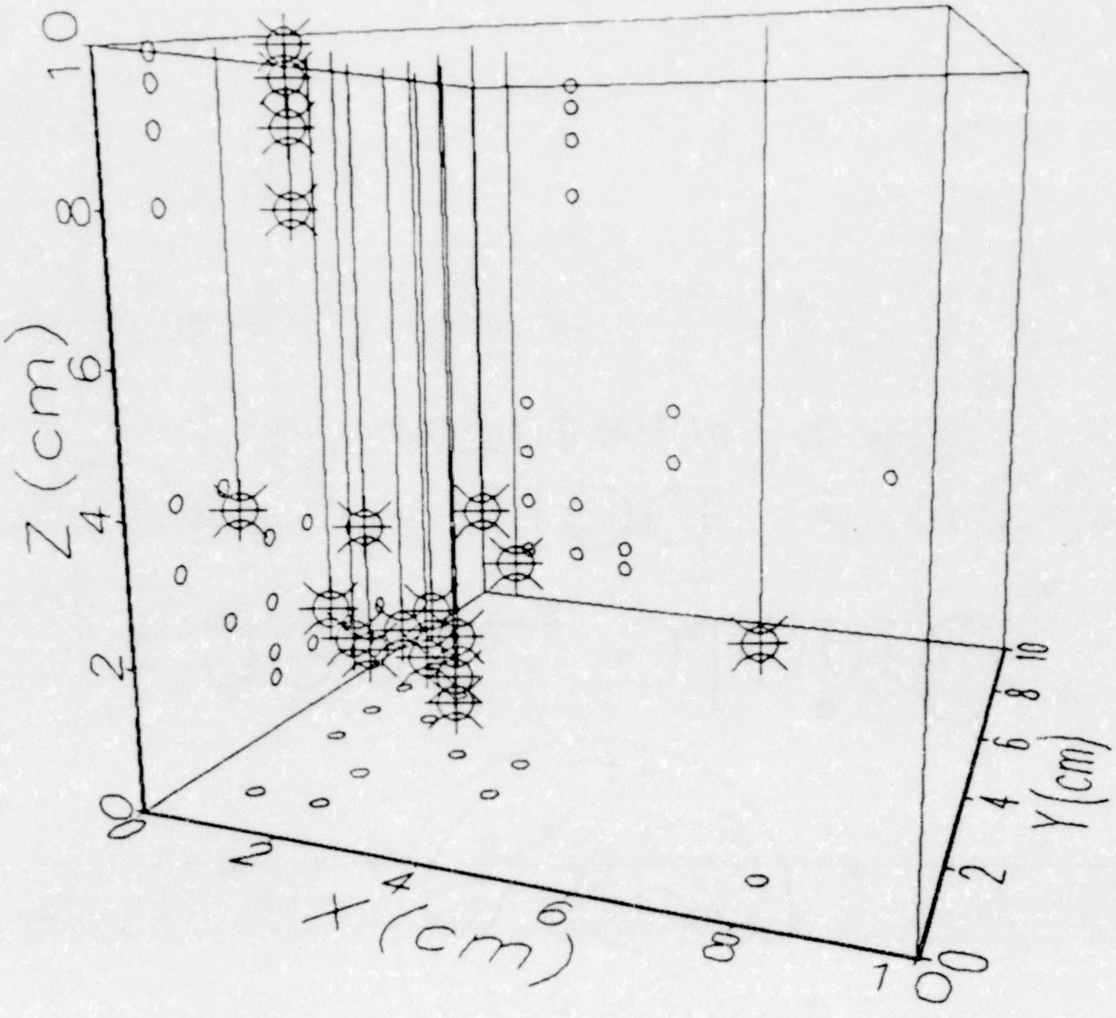
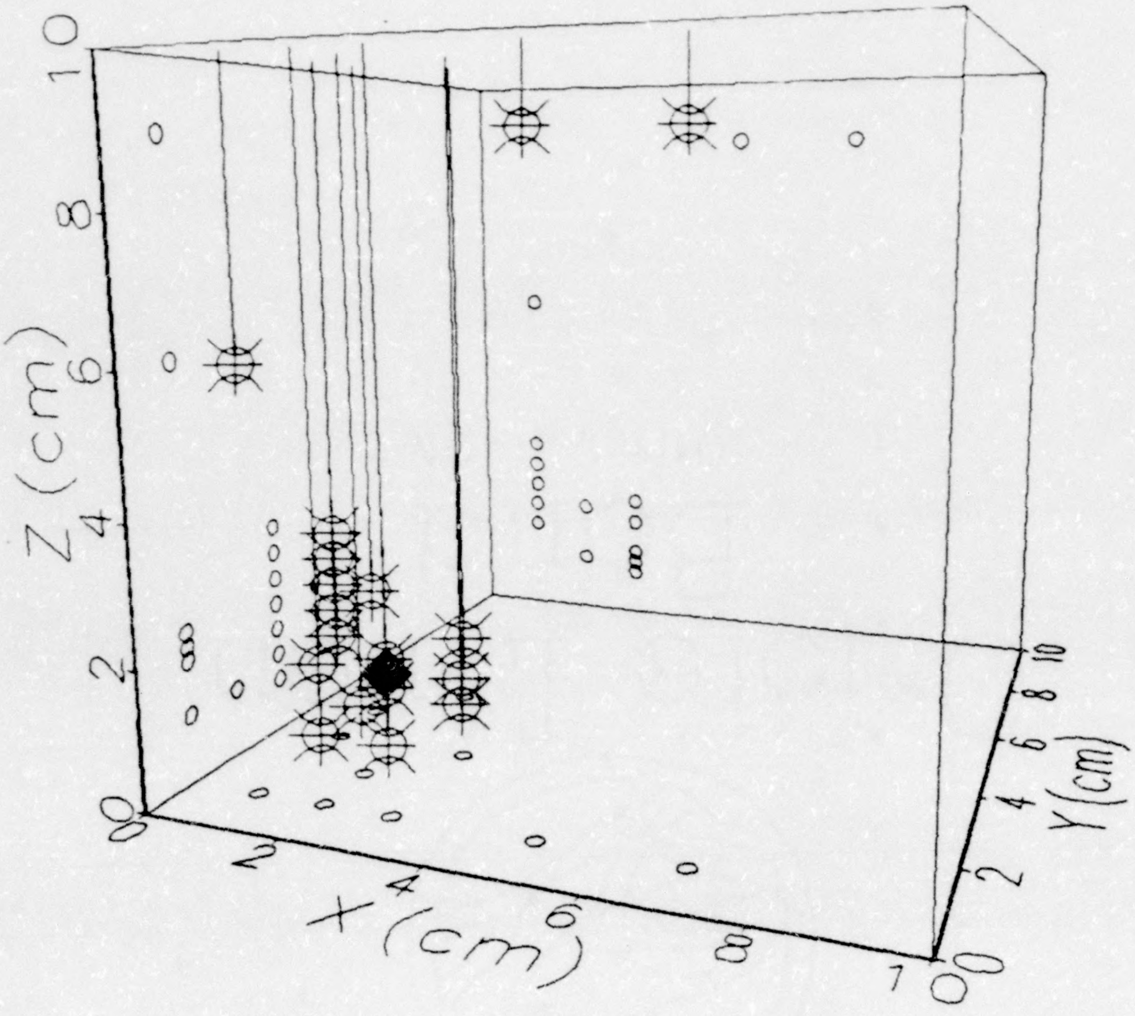

Z (cm)
0
2
4
6
8
10
X (cm)
2
4
6
8
10
Y (cm)
0
2
4
6
8
10

Figure 4. Typical experimental cage 10 minutes after feeding with *Tribolium confusum* beetles. The prey is represented by a black diamond


Z (cm)
0
2
4
6
8
10
X (cm)
0
2
4
6
8
10
Y (cm)
0
2
4
6
8
10

Walcott (1963) showed that the amplitude of a vibration in a strand of *Achaearanea tepidariorum* web decreases as the distance from the source increases. This attenuation has been measured between 1.2 and 1.5 db/cm. The average *Achaearanea* web has strands of about 20 - 30 cm and, due to probable added attenuation caused by adjoining strands, the attenuation across the length of the longest strands is probably in excess of 45 db's. Adult *S. triangulosa* webs probably respond similarly because they are similar in structure to *A. tepidariorum* webs. It is not known how juvenile webs would compare with respect to the rate of attenuation, but it seems likely that the difference would be a matter of scale in relation to the diameter of the silk strands.

Walcott's (1963) physiological work with the metatarsal lyriform organ suggested that there is a threshold of response, beyond which action potentials will not be produced. It can be concluded that on a relatively uniform tangle web, distant spiderlings will be less likely to respond to vibrations on the web than closer ones because of the attenuation of the signal. This may explain why the average response of spiderlings was less as the distance from the prey increased.

The tangle web of the Theridiids is thought to be an important preadaptation to social organization because a vibratory stimulus on any part of the web can be transmitted to a large number of spiders simultaneously and through this promote group efforts in prey restriction and feeding (Kullman 1972). Orb webs, however, are functionally designed to be occupied by individual spiders, a situation which promotes territoriality rather than cooperation. Only one group-living orb weaver, *Eriophora bistrata* has been found that exhibits communal prey capture and feeding (Uetz 1986).

CHAPTER 4

EFFECT OF PREY SIZE

INTRODUCTION

Burgess (1979) suggested that in *Mallos gregalis,* a spider which exhibits typical prey capture behavior of communal-nonterritorial species, larger prey are attacked and fed on by more spiders, as a result of the stronger vibrational cues. In the communal spiders *Anellosimus eximius* and *M. gregalis* the number of spiders attacking a prey item was less than the number feeding on it (Nentwig 1985, Burgess 1979).

An experiment was conducted to determine if the number of juvenile *S. traingulosa* attacking a prey item on the juvenile web increases with the size of the prey item, and how many spiders feed on a prey item in relation to the number that attack and assist in capture. The predatory behavior observed in the experiment is compared with that of communal adult species, from descriptions in the literature.

METHODS AND MATERIALS

This experiment was conducted between December 16 and January 9, 1991. Egg cases were taken from gravid females in the laboratory and handled in the same manner as in Experiment 1. When all spiderlings had emerged from an egg case, they were placed into the 1000 cm^3 plexiglass experimental cages in groups of ten. Egg cases were used as they became available. There were eight replications. The tops of the cages had five evenly spaced holes, 4.5 mm in diameter, for feeding purposes. There were usually enough spiderlings to fill three cages from each egg case, as egg cases contained an average of 38 (n = 43, range 16 - 67) eggs. Each of the three cages was assigned to one of three size categories of prey.

The prey used were laboratory reared *T. confusum* larvae. Small prey were 1.0 - 2.0 mm long, medium sized prey were 4.5 - 5.5 mm long and large prey were 6.0 - 7.0 mm long. In order to estimate the mass of an average prey item in each size class, 20 prey items in each length class were weighed using a Mettler H20 chemical balance. Larvae in the small prey category were too tiny (approximately 0.19 mg) to weigh individually, so 20 larvae were weighed together and the result divided by 20.

Eight trials of each treatment were conducted and each trial constituted the offspring of a different mother. The cages were then left for three days in order for the spiderlings to build a communal web. It usually took one to two days from when the first spider emerged to when they were all out of the egg case. Feeding trials were conducted between 1800 h and 2200 h on the third day after the spiderlings had emerged. By the third day, the cage was so densely filled with fine web strands that a prey item dropped anywhere in the cage would usually become ensnared in the web. Occasionally, the prey would fall through the web without becoming ensnared. In these cases, the cage was gently inverted to allow the prey to fall back into the web. Prey items were dropped into the cage through the feeding hole that was nearest the densest aggregation of spiderlings.

A constant record of the movements of the spiderlings was kept using a voice recorder for at least an hour, or until movement around the prey had ceased which usually coincided with the prey being immobilized. Note was taken of any spiders that attacked the prey. Attacking involved the observation of wrapping behavior or biting. Occasionally spiderlings would contact the prey with their front legs but not aid in wrapping or biting. These spiderlings were not counted among those that attacked. Soon after the prey was immobilized the spiderlings ceased attacking and began feeding. It was then noted how may spiderlings were feeding.

Behavior where spiderlings attempted to wrap or chased each other was considered agonistic and recorded. Agonistic encounters usually started with body-shaking and leg-drumming, which are similar behaviors to those described by Christenson (1984) for *Anelosimus eximius* juveniles. These were too frequent and subtle to record using a voice recorder.

After the initial observation period, the spiders were checked every hour to see if any additional spiders had begun feeding. Theridiids usually cut a prey item from the web when they are finished feeding. When the prey item was seen at the bottom of the cage the observations ceased. The obviously bloated appearance of the abdomen confirmed if a spiderling had been feeding.

An analysis of variance was conducted for the mean numbers attacking and for the mean numbers feeding. The means of the total number of spiderlings that attacked the prey and the total number that eventually fed for the eight trials, were compared for significance for each treatment using the LSD (least signifcant difference) method (Ostle and Mensing 1975).

Average spiderling mass was estimated as 0.28 mg by weighing

48 spiderlings and dividing by 48. The average prey mass was then divided by the average spider mass for each size class and plotted against number of spiderlings attacking and feeding.

RESULTS

For the three size classes of prey there were highly significant differences among the mean number of spiderlings attacking (Table 3 and Figure 5). The average number of spiderlings attacking small prey items was 1.86 whereas the average number attacking large prey items was 7.00. The difference between the average number feeding on small prey and medium prey was highly significant ($P < 0.01$) and the difference between the average number feeding on medium prey and large prey was significant ($P < 0.05$). An average of 1.14 and 4.63 spiderlings fed on small and large prey, respectively. For all prey sizes, the average number that attacked was greater than the number that fed, but these differences were significant only for the small and large prey sizes.

When fed small prey, groups of spiderlings seemed to be engaged in almost continuous agonistic behavior at the prey site. This would continue after the prey was dead. During the first hour of voice recording of a single group of spiderlings that had been fed small prey, 11 incidences of agonistic behavior were recorded that lasted more than 30 seconds. Incidences lasting less than 30 seconds were so numerous that they could not be easily counted. When fed large prey, incidences of agonistic behavior were rare and never continued after the prey was dead. In one hour of recording a group that had

Table 3. Means, ranges and standard errors of the numbers of *Steatoda tringulosa* spiderlings attacking (A) and feeding (F) on *Tribolium confusum* larvae of three different length classes.

Number of Spiderlings Attacking an Feeding						
Size class	Small 1.0 - 2.0 mm		Medium 4.5 - 5.5 mm		Large 6.0 - 7.0 mm	
	A	F	A	F	A	F
Number of Trials	7	7	8	8	8	8
Mean	1.86*	1.14**	4.00*	3.13**	7.00*	4.63**
Range	1 - 3	1 - 2	2 - 6	1 - 6	4 - 9	2 - 9
Standard error	0.26	0.14	0.46	0.52	0.66	0.89

ANOVA for Attacking- $P < 0.001$, ($F = 25.9$, d.f. 2, 20)

ANOVA for Feeding- $P < 0.05$, ($F = 7.1$, d.f. 2, 20)

* $P < 0.01$ for all comparisons

** $P < 0.01$ for Small and Medium, $P<0.05$ for Medium and large

Differences between A and F: $P<0.05$ for Small and Large, not significant for Medium

Figure 5. Number of *Steatoda triangulosa* spiderlings attacking and feeding on three different sizes of *Tribolium confusum* larvae.

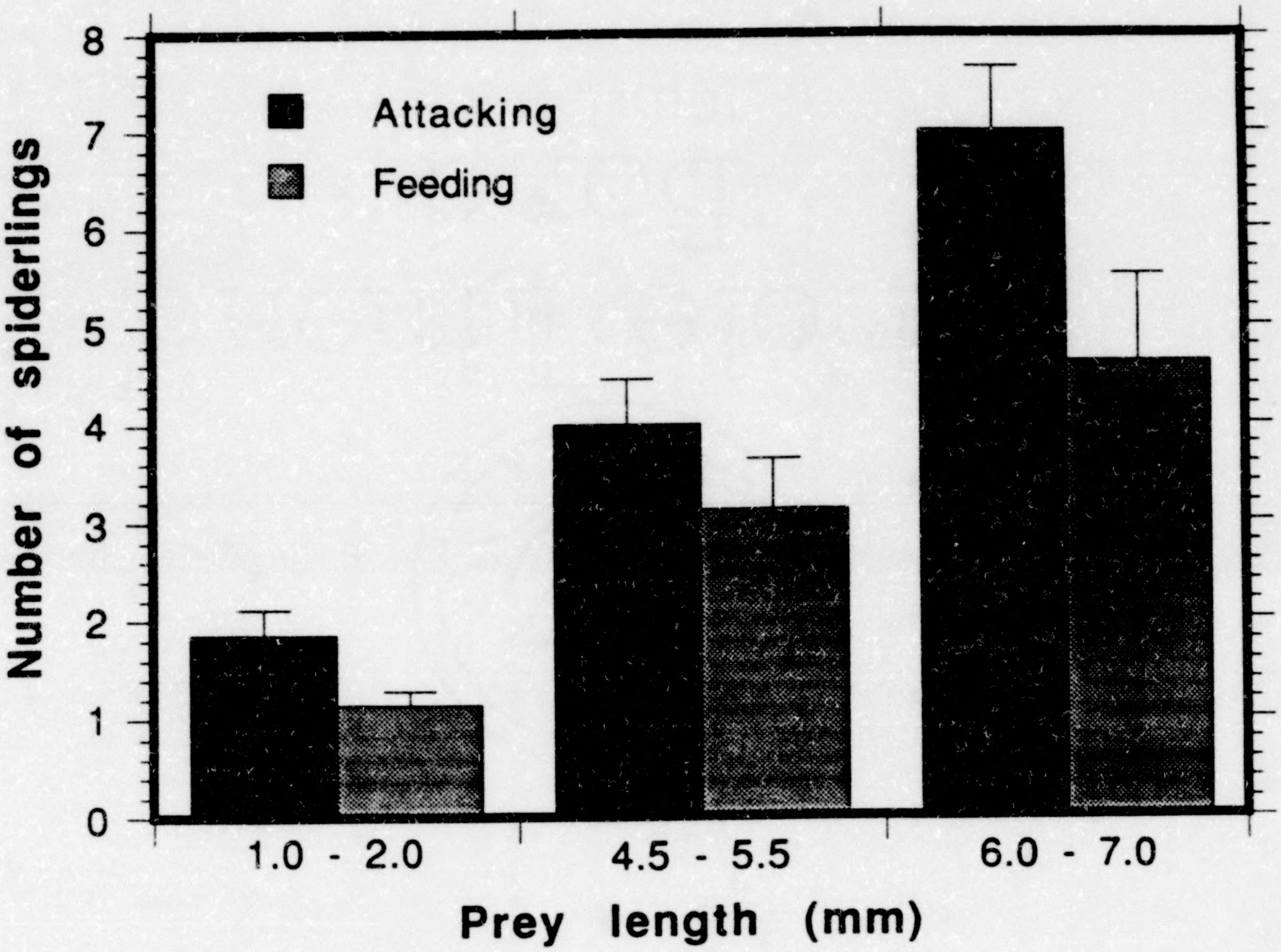
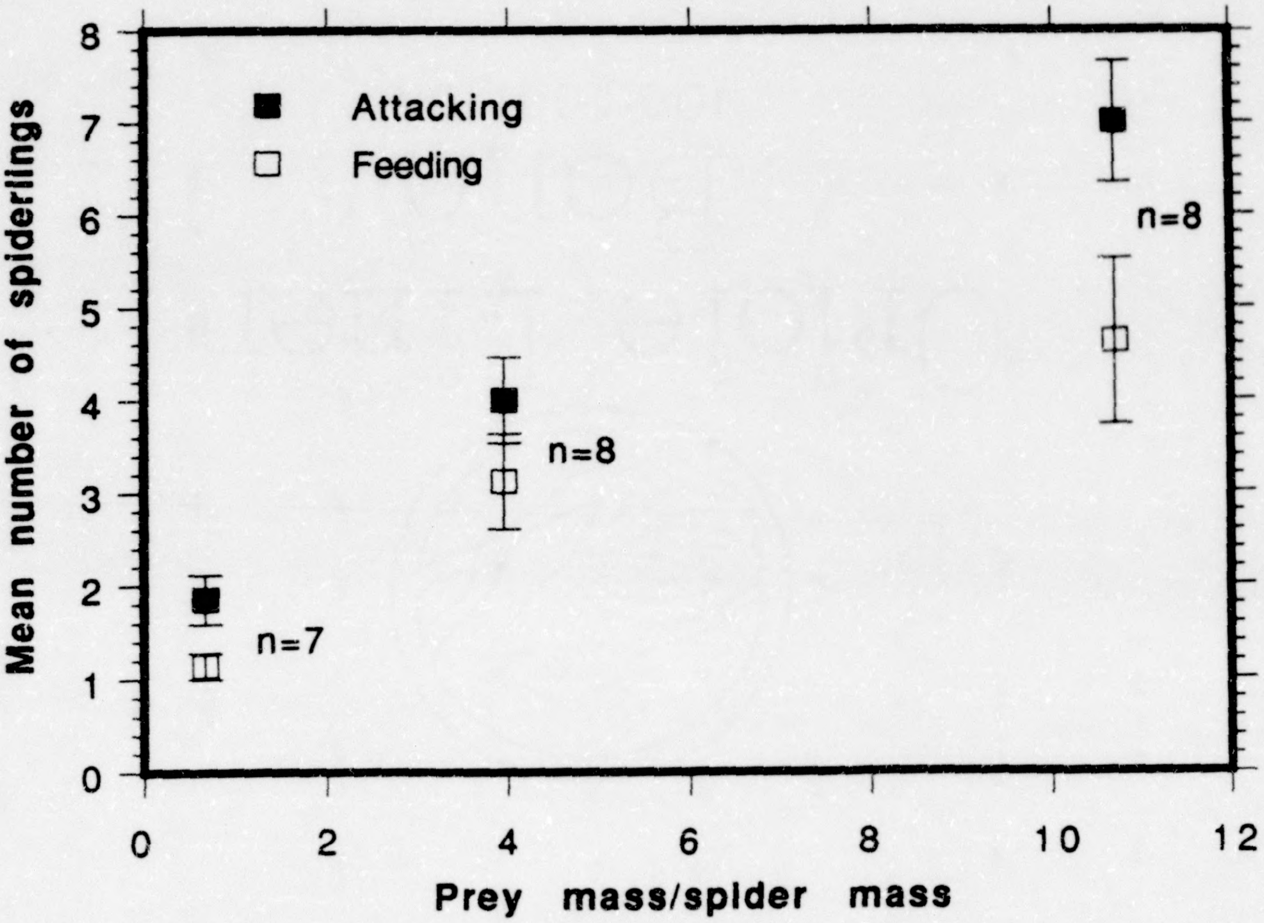

8
7
6
5
4
3
2
1
0
Number of spiderlings
■ Attacking
▨ Feeding
1.0 - 2.0
4.5 - 5.5
6.0 - 7.0
Prey length (mm)

Figure 6. Number of *Steatoda triangulosa* juveniles attacking and feeding on three different sizes of prey items against prey mass/spider mass.


Mean number of spiderlings
Prey mass/spider mass
■ Attacking
□ Feeding
n=7
n=8
n=8
0
1
2
3
4
5
6
7
8
0
2
4
6
8
10
12

been fed large prey, there were only six cases of agonistic behavior, each lasting less than 30 seconds.

DISCUSSION AND CONCLUSIONS

When groups of juvenile *Steatoda triangulosa* were fed small prey items, 1-3 spiderlings were attracted to the prey, while large prey attracted as many as nine spiderlings. In preliminary studies in the laboratory, large groups of spiderlings were seen attacking 10 mm mealworms, in groups of 20 or more. The tendency for more spiderlings to attack larger prey seemed to be similar to that exhibited in the communal attacks of adults of many permanently group-living species. Furthermore, the form that these group attacks took resembled those attacks of the adult quasisocial *Anelosimus eximius* as described by Christenson (1984) in that there was no obvious coordination of activities between individuals during their attack. *Steatoda triangulosa* spiderlings attacked in groups, flinging silk over the prey, and attempting to bite the appendages. They would avoid each other, as Christenson (1984) observed in *A. eximius*, presumably to avoid being wrapped up themselves.

The agonistic behavior that was frequently seen when groups were fed small prey resembled territoriality. A spiderling that captured a prey organism would appear to be defending it against others that attempted to feed. Perhaps the smaller the prey, the more energy the spiderlings were prepared to invest in defending it. Large prey organisms, however, had the potential to provide more food, and may have required more spiderlings to capture them. Subsequently, less energy was wasted in conspecific aggression. This behavior could be interpreted as energy based territoriality (Reichert 1978), where value of the territory increases as the size of the prey decreases, resulting in an increase in the level of aggression in defense of that territory.

Another explanation for the decrease in conspecific aggression with large prey present on the web might be that the large prey produce vibrational stimuli which override any vibrational signals coming from the spiderlings. It is likely that the small prey items, which are lighter (0.19 mg) than the spiderlings themselves (0.29 mg), provide vibrational stimuli which are too small to override conspecific signals.

In all cases more spiderlings attacked the prey than fed on them. Nentwig (1985) found the opposite effect with adult *A. eximius*. With small prey, seldom were two *S. triangulosa* wrapping at the same time. Usually, if two or more spiderlings were present at the prey together, attacks would take place in relays and the spiderling that started feeding first would drive away the others that attempted to feed at the same time. With large prey, however, there was little evidence of approaching spiders being chased by those already feeding. When the prey was large, it is not clear why some of the spiderlings that assisted in prey capture did not feed. It appeared that after prey restriction, some of the spiders would move away from the prey without any clear indication of aggression from the others. This could perhaps be considered a form of altruism, which, as defined by Wilson (1971), is self-destructive behavior performed for the benefit of others, in that certain spiderlings invested energy into prey capture but received no immediate benefit. Although the spiderlings share a large proportion of the genotype it is not known if kin selection is in operation because there is no evidence of kin recognition in spiders. Some species do not even seem to consistantly distinguish between closely related species, evidenced by the fact that *Stegodyphus mimosarum*, *Stegodyphus lineatus* and *Eresus niger* are partially tolerated by *Stegodyphus sarsinorum* when placed on the same web (Krafft 1982). However, others seem to have well developed species recognition (Kullman 1972) although precisely what sensory modalities are been used is not certain.

CHAPTER 5

COOPERATIVE PREY CAPTURE

INTRODUCTION

Burgess (1978) described cooperation in spider groups as "simultaneous co-ordination of individual's efforts on a task instead of division of labor." This implies that the spiders are performing independently of each other on the same labor, the net result being more efficient energy expenditure in the task. The main selective advantages that would promote cooperative efforts in prey capture would be decreased time and energy spent in capture and increased prey size per capture (Buskirk 1981). By being able to exploit a larger prey species through cooperative prey capture, competition with solitary species could be relieved and new niches opened.

In order to further investigate the cooperative nature of group feeding behavior in *S. triangulosa* juveniles, the following experiment was conducted. Groups of spiderlings were presented with three prey items of similar size simultaneously, with the hypothesis that if prey capture was cooperative, spiderlings would first attack one prey item as a group, ignoring the others until one was captured, provided the prey item was large enough to illicit an attack by the majority of the spiderlings.

MATERIALS AND METHODS

This experiment was conducted in February, 1991. Egg cases were taken from laboratory-reared *S. triangulosa* and handled in the same manner as in previous experiments. Ten petri dishes each had 10 newly emerged spiderlings placed in them. Petroleum jelly was wiped on the lid of the petri dishes to prevent the spiderlings from building webs on the lids. Each petri dish contained the offspring of a single mother. The egg cases of six mothers were used to ensure genetic variation. Spiderlings were allowed three days to build a communal web.

In each petri dish were placed three 6.0 - 7.0 mm *T. confusum* larvae simultaneously. The larvae were placed about 1 cm apart around the center of the dish. The spiderlings were watched for two hours or until the they ceased attacking and began to feed. The number of spiders engaged in wrapping or biting was recorded for each prey item. For each group, the prey items were ranked by the number of spiderlings that attacked. The larva that was attacked by the most spiderlings was designated number one, the larva that was attacked by the second most number two, and so on. The means for one, two, and three for the groups that responded were tested for significant differences by performing an analysis of variance (ANOVA) and then testing individual means for significance by the LSD method (Ostle and Mensing 1975).

RESULTS

When presented three prey organisms simultaneously, groups of juvenile *S. triangulosa* attacked one preferentially instead of randomly distributing themselves among the three. Table 4 presents the mean number of juvenile *S. triangulosa* that attacked. An average of 6.38 spiderlings out of a total of ten in the petri dish attacked prey. Spiderlings would attack one larva 86% of the time,

Table 4. Mean number of juvenile *Steatoda triangulosa* attacking three *Tribolium confusum* larvae presented simultaneously in eight trials.

	Number of Juveniles attacking		
	1 Larva	2 larvae	3 larvae
Mean number attacking	*5.50	*0.88	*0
Std. Error	0.66	0.35	0
Range	2 - 8	0 - 3	0

ANOVA- $P < 0.001$ ($F = 47.5$, d.f., 2, 21)

*$P < 0.001$

14% of the time they would attack two, and they never attacked three larvae. In two of the trials, the spiderlings did not respond to the prey during the two hour observation time.

DISCUSSION AND CONCLUSIONS

Tietjen (1986) reported that when several prey items were trapped on the web of the communal-nonterritorial spider *Mallos gregalis,* they became disorientated in their prey-capture behavior, as a result of conflicting vibrational stimuli as the prey items struggled. Under these circumstances, spiders turned from one prey item to another and sometimes searched within a few millimeters of a struggling fly without locating it.

Steatoda triangulosa juveniles in the laboratory responded differently than did *M. gregalis,* when presented with several prey organisms simultaneously. Single spiderlings quickly became attracted to one prey organism, usually the closest. Others moved towards that same larva, sometimes spending a few seconds probing another prey organism on the way. This continued until there were two to eight spiderlings wrapping and biting a single prey organism. During this activity, they often ignored struggling larvae only 10 mm away. That juveniles helped capture a single prey organism when several were available strongly supports the conclusion that group feeding behavior in this species is cooperative, rather than a random collective response of individual spiderlings.

In preliminary studies in the laboratory, isolated spiderlings in baby food jars were able to wrap and feed on 6 - 7 mm *T. confusum* larvae, but it took about an hour to kill the prey. Groups of three spiderlings took about 30 minutes under the same conditions, suggesting a clear advantage to group prey restriction. In the natural situation where the web is not supported on all sides as it is in a jar, prey this large probably would have escaped a single spiderling. This was confirmed when attempts to feed larvae (6 - 7 mm) to groups of juveniles on juvenile webs at the natural study site, resulted in five out of six larvae escaping before the spiderlings were able to restrict them. A single spiderling probably would be even less successful. Thus, a group prey capture effort would have a selective advantage if a prey item of the appropriate size were trapped in the web. Nentwig's (1985) studies with *A. eximius* suggested that one of the main advantages to group feeding is the ability to catch larger prey.

To begin to understand the mechanism by which this selective group attack was achieved, one may consider that *S. triangulosa* spiderlings were attracted more strongly to the combined vibrations of the struggling larvae and attacking spiderlings than to the larvae alone. It was also noticeable that larvae that were being attacked struggled more violently than those that were not and this may have presented a stimulus which was more compelling to the spiderlings.

CHAPTER 6

TOLERANCE

INTRODUCTION

One of Kullman's (1972) criteria for social organization is that organisms must display tolerance for the duration of their association. As spiders are highly aggressive and cannibalistic, suppression of these urges to form a mutually tolerant society would seem a large evolutionary step. Rypstra (1983, 1986) suggested that high prey availability is a prerequisite for the evolution of complex sociality in several spider groups.

Observations of caged juveniles indicated that for the first two or three days on the juvenile web, if undisturbed, *S. triangulosa* juveniles remained relatively inactive, did not cannibalize each other, and seemed unresponsive to each others' movements. After about four to five days after emerging from the egg case, they became more active, showing typical Theridiid agonistic behaviors such as leg-drumming, body shaking and leg-probing which are described by Norgaard (1956) and Christenson (1984). They began to disperse maximally throughout the cage, agonistic encounters increasing in frequency. After eight to ten days, spiderlings began to attack and eat each other. These increases in agonistic interactions agree with observations made by Rypstra (1986) on adult *A. tepidariorum* kept in enclosures in the laboratory. Furthermore, Rypstra (1986) found that suppression of cannibalistic tendencies and a decrease in conspecific aggression occurred in adult *A. tepidariorum* under conditions of high prey abundance.

As most of the social spider species occur in tropical areas where relative humidity is high (Riechert et al. 1986, Buskirk 1981), it was hypothesized that high humidity may also play a role in decreasing cannibalism.

An experiment was conducted to determine the effects of prey abundance and high humidity on cannibalism in juvenile *S. triangulosa* in the laboratory.

MATERIALS AND METHODS

Egg cases were collected from laboratory reared *S. triangulosa*. Once the spiderlings had molted within the egg cases, the eggs cases were weighed and placed in the centers of the experimetal cages and allowed to hatch. Egg cases of similar weights were used in the same trial. Spiderlings were left for three days after emerging from the egg case to build a communal web. At this stage the spiderlings were counted and some spiderlings were removed in order to keep group size within trials equal. Due to the large variances in clutch size (16 - 52), no attempt was made to keep the group sizes between the trials equal for fear that in removing too many spiderlings the web structure would be damaged.

There were seven trials of four treatments: High Prey, Medium Prey, Starved and Starved/High Humidity. Prey were laboratory reared *T. confusum*, 5-6 mm long. High Prey groups were fed with 1.75 prey per spiderling for the 21-days. For example, a group of 45 spiderlings received 79 prey items at regular intervals during the experiment. Low Prey groups received an average of 0.45 prey per spider for the duration of the experiment. Low Prey groups were fed on every third day, whereas High Prey groups were fed on consecutive days skipping every third day.

The High Prey, Low Prey and Starved groups were kept at an average temperature and relative humidity of 24.2 C (22 C-26 C) and 52.5% (46% - 65%), respectively, in the laboratory. The Starved/High humidity groups were kept in a growth chamber at a temperature of 24 C and an average relative humidity of 85% (82% - 87%). Humidity was controlled with open pans of water. The photoperiodic schedule for all groups was LD 16:8. Twenty one days after the initial feeding, the live spiders were counted and the cage was placed in a freezer for at least two hours in order to kill the spiderlings.

After the spiderlings were dead, the contents of the cages were analyzed. Shrivelled corpses with silk wrapping were considered cannibalized. Spiderlings whose abdomens appeared collapsed or shrivelled, but had no silk wrapping, were considered starved or desiccated. Separate ANOVA's were performed for the mean numbers of spiders that had survived, been cannibalized, or died of other causes. The means were compared and tested for significance using the LSD method (Ostle and Mensing 1975).

The spiderlings that were alive at the end of the experiment were measured, using a stage micrometer and a dissecting microscope. For 128 spiderlings, the lengths of the cephalothorax and the last two leg segments of a front leg were measured. These two measurements correlated positively. For the rest of the measurements, only the legs were measured, because they were easier to measure accurately. The lengths of the last two leg segments were very consistent within an instar. Total length of the spiderlings was measured and checked for correlation with the number of prey items fed to a group The means of the total lengths for all treatments were compared and tested for significance using the LSD method, and then used to indicate how satiated the spiderlings were.

RESULTS

The data for the average length, percentages of spiderlings cannibalized, percentages that survived and those that died of undetermined causes, after 21 days under three treatments, are presented in Table 5. Table 6 shows the levels of significance for all possible combinations of treatments using Student's t test.

The average number of prey on which each spiderling fed in the Low Prey group was 0.42 prey organisms per spiderling out of the 0.45 that was supplied. The High Prey group ate an average of 1.47 prey per spiderling, out of the 1.75 supplied.

The differences in lengths of the spiderlings for the Starved, Low Prey and High Prey were all highly significant. However, the difference between the starved group at an average relative humidity of 52% was not significantly different from the starved group kept at an average relative humidity of 85%.

Percentage cannibalism decreased as prey abundance increased for the lower (52%) humidity groups (Table 5 and Fig. 5). The differences in percentage cannibalized between Low Prey and High Prey were nearly significant ($P < 0.1$), and the differences between Starved and Low Prey was significant at $P < 0.05$. Spiders of the Starved/High Humidity group showed a large decrease in cannibalism over Starved groups under normal humidity. The Starved/High Humidity

Table 5. Response of caged *Steatoda. triangulosa* spiderlings to treatments of Starvation, Low Prey, High Prey and Starvation under High Humidity, after 21 days.

	Starved		**Low Prey**		**High Prey**		**Starved/High Humidity**	
	mean	SE	mean	SE	mean	SE	mean	SE
Prey Supplied per Spider	0	0	0.5	0	2.0	0	0	0
Prey Fed upon per Spider	0	0	0.42	0.36	1.47	0.08	0	0
Average Length (mm)[a]	0.94	0.02	1.21	0.02	1.40	0.0	0.91	0.01
Percentage Cannibalized[b]	47.5	6.2	24.1	5.1	12.4	4.1	12.1	5.3
Percentage Other Mortality[c]	24.2	3.9	12.9	4.9	4.2	1.6	21.6	9.0
Percentage Survival[e]	28.3	4.4	63.3	7.2	82.9	5.0	69.4	10.8
Total Percentage of Survivors reaching Third Instar	5.1		32.4		61.4		2.3	

[a] ANOVA- $P < 0.01$ ($F = 181.9$, d.f., 3, 464.)

[b] ANOVA- $P < 0.01$ ($F = 9.2$, d.f., 3, 21)

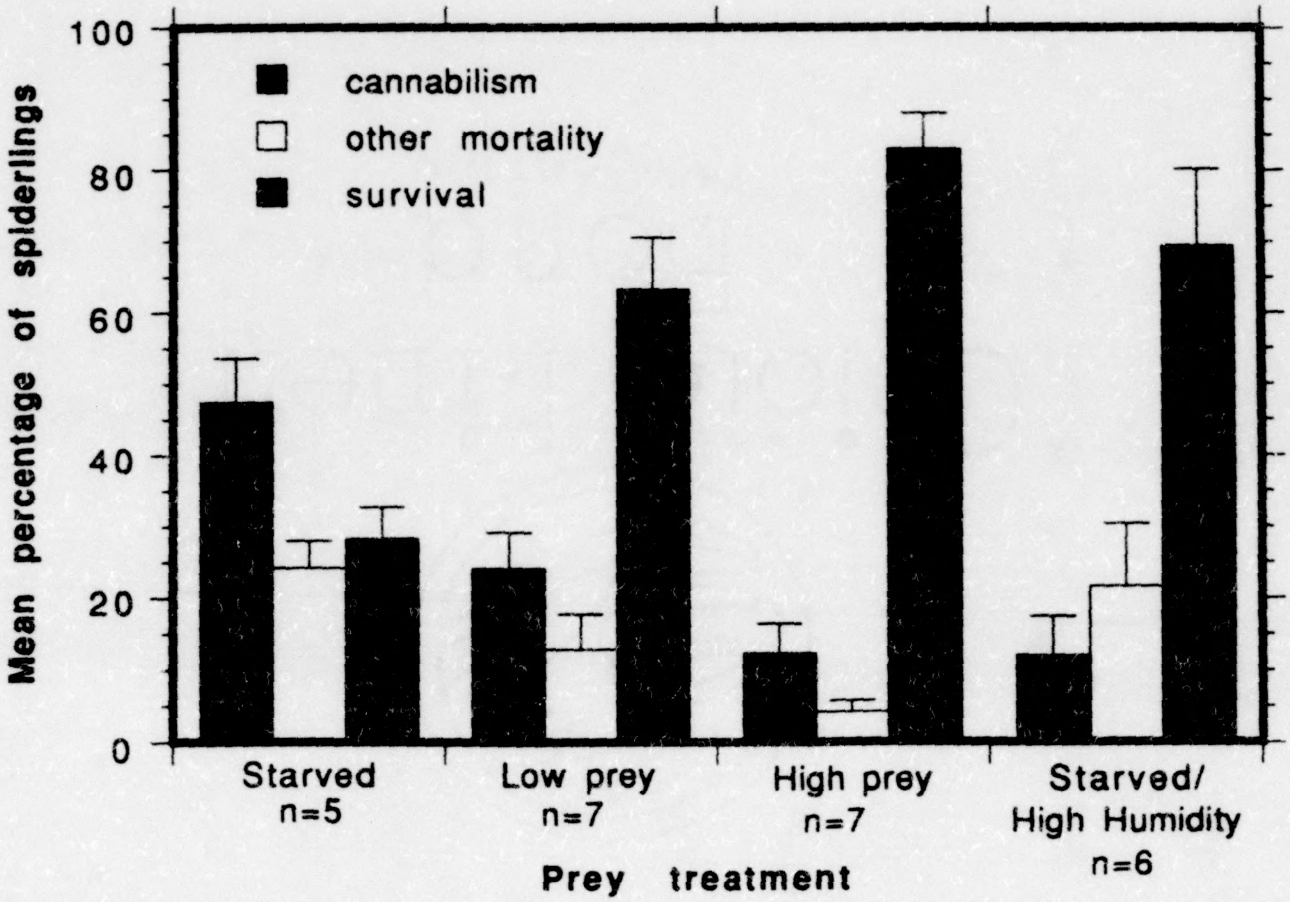
[c] ANOVA- $P < 0.1$ ($F = 2.8$, d.f., 3, 21)

[d] ANOVA- $P < 0.01$ ($F = 8.8$, d.f. 3, 21)

Table 6. Levels of significance for the mean responses of caged *Steatoda triangulosa* spiderlings, to treatments of Starvation, Low Prey, High prey and Starvation under High Humidity for all possible combinations of treatments, using the least signifcant differences method (LSD) (Ostle and Mensing 1975).

	Low prey	High prey	Low prey/High humidity
Average length			
Starved	$P < 0.01$	$P < 0.01$	NS
Low prey		$P < 0.01$	$P < 0.01$
High prey			$P < 0.01$
Percentage cannibalized			
Starved	$P < 0.05$	$P < 0.01$	$P < 0.01$
Low prey		$P < 0.1$	$P < 0.1$
High prey			NS
Percentage 'other mortality'			
Starved	NS	$P < 0.05$	NS
Low prey		NS	NS
High prey			$P < 0.05$
Percentage survival			
Starved	$P < 0.01$	$P < 0.01$	$P < 0.01$
Low prey		NS	NS
High prey			NS

Figure 7 Mean cannibalism, 'other mortality' and survival rates of juvenile *Steatoda triangulosa*, kept in enclosures under conditions of Starvation, Low Prey, High Prey and Starved/High Humidity.


100
80
60
40
20
0
Mean percentage of spiderlings
■ cannabilism
☐ other mortality
■ survival
Starved
n=5
Low prey
n=7
High prey
n=7
Starved/
High Humidity
n=6
Prey treatment

groups had an average percentage cannibalism of 12.1% which was remarkably similar to the average percentage cannibalism under High Prey conditions (12.4%).

The percentage that died of undetermined causes (ie., Other Mortality) showed significant differences ($P < 0.05$) between Starved, (lower humidity) and High Prey, and between Starved/High Humidity and High Prey.

Average percentage survival increased as prey abundance increased under lower humidity conditions, although the difference between Low Prey and High Prey was not significant. Starved/High Humidity was highly significantly different than Starved under lower humidity. There were no other significant differences. The percentage of surviving spiderlings that had reached the third instar by the conclusion of the experiment was approximately proportional to prey consumed in all groups, regardless of humidity levels.

DISCUSSION AND CONCLUSIONS

The Low Prey groups fed on approximately 93% of the prey that were supplied, whereas the High Prey groups fed on approximately 85% of the total prey supplied. The 7% of the prey that the Low Prey groups did not feed on probably avoided capture by falling to the bottom of the cage where they could not be reached. The High Prey groups fed on about 3.5 times as many prey organisms as Low prey groups did. From this I concluded that the Low Prey diet was probably sub-optimal, while the High Prey groups were probably close to prey saturation.

The average length of the surviving spiderlings was used an an estimate of how much they had eaten because the majority of the length differences were due to distention of the abdomen. Thus, the amount of prey fed on was reflected in the total lengths of the spiderlings. The number of spiderlings reaching third instar was used as an estimate of actual growth. This again reflected the amount of prey fed on.

In the Starved groups, there were no significant differences in either the average lengths of spiderlings or the percentages of spiderlings that reached third instar. It might be thought that the high rate of cannibalism in the Starved lower humidity group would result in some distention of the abdomen and subsequent growth. However, the total mass fed on by a Starved group that had a 47% rate of cannibalism would be 14 mg, which is significantly less than the mass of prey fed on by a group of 30 spiders in a High Prey treatment at about 134 mg, and that of a Low Prey group about at 38 mg. Even on this proportionately lower mass of available food, one might expect some additional growth over the high humidity group which had a cannibalism rate of only 12.1%. This may be explained by the increased rate of desiccation in the lower humidity groups resulting in loss of fluids and subsequent loss of mass.

The unexplained mortalities may have been due to desiccation or starvation, or both, judging from the appearance of their abdomens which were in varying states of crenation. There were also fewer cases of unexplained mortality as the prey levels went up. It would seem that cannibalism is reduced under conditions of high prey abundance and high humidity. As spiders are fluid (Comstock 1948) feeders and probably derive most of their water from their diet, the effects of hunger and desiccation may be synergistic in increasing intraspecific aggression in juvenile *S. triangulosa*, resulting in increased cannibalism.

CHAPTER 7

CONCLUSIONS

CONCLUSIONS

TOLERANCE

Before a phylogenetic move from asocial to social can occur, organisms have to be tolerant of each other (Kullman 1972). Suppression of predatory responses towards conspecifics requires that conspecifics are able to be recognized and Kullman's (1972) studies clearly indicate that this is possible. Tietjen (1986) suggested that vibrational and/or chemical cues are able to reduce intrapecific aggression. In addition, Rypstra's (1983, 1986) data, and my data, suggest that increasing prey abundance decreases conspecific aggression and cannibalism.

High relative humidity, as suggested by the present study, could play an indirect role in increasing tolerance by reducing the amount of water lost through evaporation. As *S. triangulosa* thrive in domestic environments, they probably are not dependent on external drinking water, getting most of their water through feeding. Thus, predatory behavior would be activated more readily in low humidity environments and tolerance would persist longer in more humid areas. Furthermore, the rate of desiccation is probably greater in juveniles than in adults, due to a higher surface area to volume ratio. It may be that desiccation is a primary motivation to feed, particularly in juveniles. It can be concluded that the effects of prey abundance and humidity are probably synergistic in promoting tolerance. These conclusions are supported by the fact that all social spiders live in tropical or subtropical areas (Buskirk 1981) which are characterized by high prey abundance (Rypstra 1986) and high humidity (Riechert et al. 1986).

COOPERATION

Wilson (1971) and Kullman (1972) identified cooperation as an essential criterion for sociality. The nature of cooperation and the subsequent degree of social organization can be deduced from the mode of intraspecific communication involved (Witt 1975). Communication in biological systems must be carefully considered according to the organisms with which one is working. Wilson (1975) defined communication as "the action on the part of one organism that alters the probability pattern of behavior in another organism in a fashion adaptive to either one or both of the participants." This broad definition encompasses even the most simple systems such as a flower attracting an insect.

Cooperation can be highly developed, involving complex communication and/or extreme altruism, as found in the eusocial insects, or it can be much simpler, such as the kind of cooperation that characterizes group-living spiders. This takes the form of 'mass action' behavior in which behaviors are not highly coordinated, but proceed through indirect interaction of colony members (Wilson 1971). This is the kind of behavior seen in cooperative web building in social spiders (Tietjen 1986), and it appears to be the same in communal web building by juvenile *S. triangulosa*, where spiderlings that had just emerged from the egg cases moved around rapidly, dragging their silk lines creating a communal web as the gross result of their individual wanderings. Superficially this web appears to be a random collection of fine silk strands, but on close inspection it seems to be similar in general structure to the adult web.

Group prey capture might also be considered a mass action behavior, but the experimental work presented suggests that it is greatly modified depending on the context in which it occurs. The data suggest that the size of the prey organism plays an important role in determining how many individuals become involved in the prey capture and the degree of conspecific aggression that occurs at the prey site. Small prey invited attacks by small numbers of spiderlings and promoted territorial behavior, while large prey invited large groups of cooperative attackers. One of the functions of territoriality is to insure access to resources, and when resources are abundant territoriality breaks down (Morse 1980). The data from this study suggest that small prey items represent a limited resource to a group of juvenile *S. triangulosa* resulting in an increase in territoriality and that large prey represent abundant resources promoting cooperative feeding. Carpenter and MacMillan (1976) found that nectar feeding birds shift from territorial to non-territorial behavior in conditions of high food abundance.

The tendency of spiderlings to attack in numbers proportional to the mass of the prey may be a result of the properties of spider web strands to transmit vibrational stimuli. Walcott (1963) suggested that due to attenuation, a vibrational signal transmitted through the medium of the web will be receptive at distances proportional to the original strength of the signal. If one assumes that strength of the original signal depends largely on the mass of the insect caught in the web, then it is reasonable to assume that a larger prey organism will communicate its presence to a larger number of spiderlings. It would be interesting to investigate whether the number of spiderlings attracted to the prey is proportional to the amount of available energy in the prey source, which would further clarify the adaptive significance of the behavior.

INTERATTRACTION

True interattraction has not been shown for spiders, and it is not certain whether it exists in the same sense as it does in social insects However, Kullman (1972), with *Stegodyphys sarasinorum*, and Krafft (1982), with *Agelena consociata*, have shown that after spiders that had been previously isolated were placed into a container together they clumped in several groups after a short time. Similar experiments conducted by me with *S. triangulosa* juveniles showed clumping into one to three groups. Krafft (1982) suggested that the silk itself is an attractant for spiders and would promote group cohesion. The clumping behavior observed by Krafft (1982) and me may be related to the tendency of spiderlings to climb. The first spider that was able to secure a web strand to the wall of the container would supply an easy scaffold for the next to climb up and attach further web strands, and so on. It is likely, therefore, that it is the web structure in combination with ecological factors such as relative humidity and prey abundance that promote group cohesion.

ROUTES TO SOCIALITY

The parasocial route from solitary existence to social living, in which parental care is extended, thus delaying dispersal of offspring has been proposed by Kullman (1972) for the Theriidae. Hirschberg (1969) described the stages in the evolution of broodcare to explain how this may have come about. Rypstra's (1986) study suggested that the sub-social route, where individuals of any age aggregate around a common resource, may be postulated for this family under appropriate ecological conditions. It may be that in any species both pathways could operate with varying emphasis (Buskirk 1981).

My studies indicate that *S. triangulosa* possesses certain behaviors that suggest an early stage enroute to sociality, which combines features of both the parasocial and sub-social routes. The juvenile phase may be prolonged, not by maternal care, as suggested by the parasocial route, but through the extension of the group feeding stage. The factors that might promote this extension would include 1) the presence of abundant prey of the correct size, which would promote tolerance and cooperation, and 2) environmental conditions such as persistent high relative humidity, which would further enhance tolerance by decreasing the predatory urges. These factors are facilitated by the structure of the typical Theridiid web, and it's ability to communicate the presence and relative size of a prey organism to many colony members simultaneously.

There are other factors, however, which may suppress social development in this species. Juvenile *S. triangulosa* seem to be relatively precocial, when compared with other species. For example, they are much larger as second instars than juvenile *A. tepidariorum*. This may be why they are able to feed immediately after emerging from their egg cases, unlike the species that perhaps prompted Burgess (1976) to state that juveniles on the communal web do not feed. Furthermore, their ability to feed at emergence may be the reason that they have a relatively short juvenile phase (1-3 days) when compared with *A. tepidariorum* (13 - 14 days), (Valerio 1977).

Steatoda triangulosa produce the same number of eggs per egg case as one might expect from a social species, according to Buskirk's (1981) observations. However, this may not represent a preadaptation to sociality but rather evidence that this species is relatively K - selected compared to other solitary species. Spiders employ a range of strategies to ensure the survival of enough young to maintain a stable population. These include maternal feeding, where mothers regugitate food to their young (Kullman 1972, Ito 1985); egg feeding, in which juveniles in the egg case eat unviable eggs (Valerio 1974); gerontophagy, where the mothers that are beyond reproductive age are fed on by juveniles (SeiBt and Wickler 1987); and high fecundity, typified by *Latrodectus* (Thorp and Woodson, 1945). The production of precocial young may represent another strategy.

The presence of the behavioral traits described in this study indicate that *S. triangulosa* appears to have several preadaptations to a permanently social mode of existence, coupled with others that preclude the formation of a society. Environmental factors play a large role in promoting or suppressing such traits. Many spider species show considerable flexibility in spatial organization in response to environmental conditions such as prey abundance (Rypstra 1986, Gillespie 1987, Uetz et al. 1982), and it is ultimately these factors that will operate through natural selection to dictate the level of social organization of a species.

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