Social behavior in spiders

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Introduction

Social behavior is rarely observed in spiders. Merely twenty five to fifty species of the approximately 38,000 known species can be defined as either social or subsocial (Avilés et al., 2006; Johannesen et al., 2006; Salomom and Lubin, 2007). Social spiders occupy communal nests which can contain several to thousands of individuals. Subsocial spiders are those that demonstrate extended maternal care into the juvenile period, but the young leave the nest as they reach adulthood, and then undergo and solitary phase. Some spiders, such as the *Anelosimus studiosus*, vary their social behavior across latitudinal ranges. Adult females of this species, which live at higher latitudes will exhibit social behavior. However, females living in the lower latitudinal ranges prefer to be solitary. (Jones and Riechert, 2008; Pruit et al., 2008; Riechert and Jones, 2008)

Right now it is believed that complete sociality in spiders developed via the subsocial route, i.e. spiders that have evolved to a social status, began the evolutionary process with extensive maternal care. Mothers that exhibit this extended care typically feed the young with digested food that she has stored in her body. Then the young commit matriphagy, consuming the mother. (This is true in most cases but not in all. Some species will have more than one brood)(Jones and Riechert, 2008; Pruit et al., 2008; Riechert and Jones, 2008). They remain in the nest for a period of time and forage communally until they reach subadult or adulthood.

There are, of course, advantages and disadvantages to being a social spider. Advantages can include: protection against predators, increased size of prey, overall colony survival rate, decreased silk costs or and alloparental care (care given by a female that is not the mother). Disadvantages can include: competition for prey, fewer reproductive females per increased colony size, decreased female size or dimorphism and parasitic infestation by other spiders. This review article will discuss current research done in the area of the evolution of sociality in spiders.

Cooperation in prey capture and feeding behaviors

Kin recognition

Food is a fairly important concept when you are a spider. How much biomass a spider has available to it determines, in most species, how large it grows. Size is directly correlated to a spider's fitness (Salomon et al.,2008; Yip et al.,2007). Spiders digest their food externally by spitting digestive enzymes into the body cavity of the captured prey. They then ingest the liquefied contents.

Spiders that live communally tend to hunt together and share the prey. This process of sharing can lead to cheaters, those spiders who eat but don't invest their own digestive enzymes. One way to minimize the number of cheaters is to engage in kin recognition. Schneider and Bilde (2008) investigated the dynamics of kinship and cooperative feeding behaviors in *Stegodyphus lineatus*. *S. lineatus* is a subsocial spider that inhabits arid climates around the

Mediterranean. These spiderlings will remain in the natal nest for one to two months after matriphagy and hunt and feed together.

By dividing their experimental groups into; siblings, familiar non-siblings and non-siblings who were not familiar with each other, Schneider and Bilde (2008) were able to determine the difference in feeding efficiency between these groups. They found that not only did the siblings gain more weight than either of the other two unrelated groups; they also extracted more mass from the prey and had a lower mortality rate.

There was not a significant difference in feeding efficiency between the familiar non-siblings and the non-familiar non-siblings, indicating that relatedness indeed increases feeding efficiency. Producing digestive enzymes is costly, and in some species it takes longer for groups to digest prey than it does for an individual. Thus, in general, group feeding is less efficient than solitary feeding. Siblings are less likely to withhold their own digestive enzymes because the survival of a sibling may mean the survival of a gene. (Schneider and Bilde, 2008)

Stegodyphus lineatus, although subsocial, is capable of extending its social phase into adulthood if food sources are sufficient. Cannibalism is common across spider species both in sexual and non-sexual frameworks. It is more likely to occur when food sources are scarce. Kin recognition may be a significant factor in deciding whether or not to cannibalize. Bilde and Lubin (2001) observed that *S. lineatus,* when starved, tend to be more cannibalistic when placed in non-sibling pairs than when paired with a sibling. However, cannibalism only took place in this species when they were starved and not at any other time. These authors discussed a social crab spider, *Diaea ergandros*, of which the subadult female will eat her brothers and an unrelated female, but leave the unrelated males alone, maximizing her opportunity for outbreeding.

The concept of kin recognition is important for social spiders because young spiders tend to remain in the communal web, and only occasionally leave the natal nest. This increases the likelihood of inbreeding, and potentially decreases the fitness of the entire community. So the ability to simultaneously preserve a genetic line through the process of cooperation but also increase genetic diversity by way of reduced inbreeding should extend the life of a species.

Kim et al. (2005) looked at cooperative prey capture in another subsocial spider, *Amaurobius ferox.* They determined the mechanism behind their behavior and also the functional value of cooperative prey capture. *A. ferox* exhibits typical subsocial behavior. After the mother is consumed, the young remain in the nest for about a month and feed together. Kim et al. (2005) compared the number of individuals it took to capture prey at increasing prey masses. Presented with prey sizes of 1, 5, and 40 mg, they found that larger groups of spiderlings could capture larger prey than individuals could; however the efficiency peaked at ten individuals.

The number of cheaters, those that did not invest digestive enzymes but later consumed the prey, increased as the number of spiders increased. This apparently agrees with a game-theory prediction on the evolution of cooperation proposed by Packer and Ruttan in 1988, but expansion on this idea is beyond the scope of this paper. (Kim et al., 2005)

Kim et al. (2005) noted that the level of aggression between spiderlings was the highest when presented a cricket of 5 mg but the behavior never resulted in mortality and a threat from one spiderling typically resulted in the retreat of the other. They also observed timing of dispersal from the natal nest and also the body mass of dispersing individuals neither of which were significantly different across experimental groups.

Kim et al. (2005) also looked at how the cooperative attack took place when a group of spiderlings was presented with prey that was ten times larger than the individual spider, thus too large for only one spider to conquer. This is worth mention because the attacks were consistent and appeared organized and systematic. The spiderlings described a specific sequence of events each time including: latency (where no visible change of behavior was observed); orientation (spiderlings turned toward the prey); movement (initiated by a "bellwether"); touching/attacking (the first was always carried out by one individual and multiple attacks were needed before seizing took place); seizing (pulling on the prey's extremities and usually carried out by the first attackers); and feeding (taking place after cessation of prey movement and a collective activity).

The first three individuals to attack represented 90% of the attacks taking place and they focused on the extremities, the legs and antennae, while the late arrivers settled on the abdomen and thorax and did not exhibit attack behavior. Communal capture of prey this large never presented with aggression between conspecifics. Observations at this level contribute to the evidence that cooperation is occurring as opposed to random, disorganized tolerance of one another.

Environmental factors influencing sociality

Most social spiders are found in and around the tropical regions most likely because the seasons support year round colony function, prey availability and the required prey quality i.e. large insects. *Anelosimus studiosus*, on the other hand shows the opposite trend.

Anelosimus studiosus lives approximately one year and is distributed from Argentina to New England. Unlike the previously described extended maternal care, this mother will regurgitate food to her young but she may have up to three broods during her lifetime. She does not sacrifice herself to her young but instead kicks them out as they become mature. Riechert and Jones (2008) documented nest sites for *A. studiosus* at 2^o intervals beginning at latitude 26^o in South Florida up to 36^o in east Tennessee. They determined that the dominant social structure is that of a solitary female. However, multifemale nests first appeared at 30^o and both the number of multifemale nests and the number of females in those nests increased as latitude increased.

In a subsequent paper, Jones and Riechert (2008) hypothesized that at cooler sites, maturation occurred more slowly and this increased the possibility of the mother dying before her brood was raised. If this happened, the other females in the nest would raise the young. They manipulated the microclimates of *Anelosimus studiosus* to test their model.

Jones and Riechert (2008) did find that colonies survived better with increased number of adult females. This in turn decreases the probability of complete colony failure. They found that each mother also had increased reproductive success because this species does not discriminate between kin and non-kin. If one mother dies the other females care for her young ensuring a direct fitness advantage.

They found that single females had the highest reproductive success at all sites. The <u>mean</u> reproductive success was higher in colonies with six or fewer females and the lowest success was found in colonies with greater than ten females. So multifemale nests do present a small advantage, and they do increase in frequency as latitude increases, but single female nests still dominate in numbers at all locations. And the question remains “Why the variation in phenotype”? We don’t know yet. (Jones and Riechert, 2008)

Because behavioral traits can have fitness consequences, Pruitt et al. (2008) tested to see if the behaviors carried out by *A. studiosus* might limit the species in shifting from asocial to social. For example if, in order to become a social species, the spider must be able to tolerate conspecifics, and tolerance is directly linked to aggressive feeding behavior, or antipredator response, these are potential fitness costs and the behaviors limit the evolution of sociality. On the other hand, the hasty reaction toward a possible predator might be too hasty and end in death for a more aggressive asocial spider and tip the evolutionary scale toward sociality. (Pruitt et al., 2008)

Individuals of *Anelosimus studiosus* who are social tend to demonstrate lower levels of activity, do not respond as intensely to prey encounters on their web, and are not as aggressive toward predators as their asocial counterparts.. All of this would suggest a pleiotropic (one gene is responsible for more than one phenotypic characteristic) relationship between the social behavior and these traits. (Pruitt et al., 2008)

In the lab, when pitting a social spider against an asocial spider in these trials, the behavioral traits here were found to favor the asocial spider as she dominated feeding rights and even cannibalized the less aggressive social spider. (Pruitt et al., 2008)

For *Anelosimus studiosus*, there are more single, asocial female nests at all latitudes. This means that they pose a threat to the social females because the asocial females will dominate the food as well as prey upon the social female, therefore limiting the evolution of sociality. (Pruitt et al., 2008)

Cooperative breeding

Individual *Stegodyphus dumicola live* for one year, there a high degree of inbreeding and some females do not mature in time to mate. These females may act as helpers in the nursery, providing alloparental care to the young.

Typically, the social nests consist of many more females than males. Salomon and Lubin (2007), looked at cooperative breeding in *Stegodyphus dumicola* to determine if non-breeding females of the nest participated in brood care, and if so, was there a fitness benefit to being raised by more than one female.

Salomon and Lubin (2007) collected field colonies and allowed the females to mate however, only one egg sac was allowed per colony so after the first egg sac hatched, they removed the rest. They counted and weighed the young, once after the first female died and again after all the females died. They also took data on single females alone with their brood.

Salomon and Lubin (2007) found that all the adult females participate in brood care and that the young in multifemale colonies were heavier than the young of a single female. Not only does the care include regurgitation, but the young raised by more females ate most of the adult females available. By having more females available, the maternal period was longer which means that more food was readily available to these spiderlings. It follows, that these spiderlings weigh more when they begin foraging, granting them a higher foraging efficiency. Furthermore, the helper females may benefit indirectly from ensuring that the young survive because there is such a high degree of inbreeding in social colonies.

Salomon et al. (2008) asked why some of the females in the *Stegodyphus dumicola* colony might not reproduce. They wanted to know if nutrition played a role in how females developed. They compared the effects of lipid rich and protein rich diets on the colony population and determined that lipids play a vital role in the maturation of a female.

Although social spiders hunt and feed together, there is not necessarily always enough prey. Competition is always taking place. Quality and quantity of food could be what decides the skewed reproduction in the colony. Unequal distribution of prey items can lead to unequal growth and development of the female. Also, because eggs must have all the nutrients to support the embryo, quality of diet is important in egg development.

It has been shown that when juvenile spiders of *Stegodyphus lineatus* are deficient in a nutrient, they are able to extract that specific nutrient from the liquefied body of the prey. If this nutrient selection is occurring in competing reproductive females, then it is likely that some are not getting enough of the correct nutrients for egg development. (Salomon et al., 2008)

By comparing the nutrient composition of breeding versus non-breeding females, to what degree colony nutrition skewed reproduction, and by allowing females to feed in a noncompetitive way, Salomon et al. (2008) were able to determine what nutrients were extracted before reproduction and whether there was competition for that nutrient taking place.

Salomon et al. (2008) determined that adult females weighed more than subadult females in the colony and when they were presented with lipid rich crickets, more of the females reached sexual maturity, decreasing the reproductive skew. This was not found in the colonies that were supplemented with protein rich diets.

Salomon et al. (2008) also found that when feeding alone, subadult females extracted a higher ratio of lipids to nitrogen then did the adult females. This suggests that when given a chance, they will extract the nutrients required to mature physically and reproductively.

Extended maternal care is thought to be the first step of socialization in the arachnid. Salomon et al. (2008) suggest that the competition for prey and the nutrients within that prey required for reproductive success becomes the next step in the evolution toward sociality. Caste systems begin to evolve as the females that do not get enough nutrition benefit indirectly by becoming helpers, providing alloparental care to the young.

Dispersal

Discussed here are two reasons why a social spider might leave the natal nest. First is when a juvenile spider of a subsocial species is kicked out of the nest. Trabalon and Assi-Bessokon (2008) looked at what happens to the chemical nature of a web as the subsocial spider transitions from social to asocial. They found that the chemical signatures are different at various stages of a female's life. The signature of the web change right after the young leave the nest. When behavioral preferences were tested, the web of females who had young was unattractive to virgin females and the web of females incubating eggs was attractive to females that had just mated.

Dispersal also happens at the colony level. Yip et al. (2007) theorized that web size would follow the rule that surface area decreases per unit volume i.e. the web volume will increase to the third power but the surface area will only increase to the square power. Because many spiders sit and wait for prey to come to them, decreased surface area as the colony grows in population, would mean a possible reduction in food.

The surface area of the web does increase more slowly than the volume and the number of prey captured per capita decreases. However larger webs catch larger insects so the biomass remains the same until the web size reaches intermediate as defined, by the authors. At this point, the biomass is not enough to support the number of spiders. Social spiders do not tend to disperse until the web is large in size and this decrease in food availability as the web reaches its prey capacity may explain this timing of dispersal. (Yip et al; 2007)

Social Evolution

Why evolve into a social spider at all? With so much inbreeding in the colony how does this translate to evolutionary stability? Johannesen et al. (2006) looked at the three social species of the genera *Stegodyphus* to determine the age of the species, whether they represent an ancestral or derived state, and species diversification. They suggested that perhaps these social species are a “transient ‘dead end’ species and have not undergone diversifying speciation”.

Using six spider species, DNA was analyzed and Johannesen et al. (2006) concluded that the social species of *Stegodyphus* are indeed old and derived. They are not transient and so they are not evolutionarily unstable.

They found that the genus *Stegodyphus* is not derived from a single ancestor. They also determined that lineage divergence in the three genera remained constant but cladogenesis was limited suggesting that while the spider is able to sustain sociality, they also may be limited by environmental, and morphological factors so their only option is sociality. Johannesen et al. (2006) maintain that niche availability may be one of the limiting factors in colony evolution.

Conclusion

Sociality in spiders is rare. With so few fully social species and with species in the subsocial stages, spiders are ideal to study the evolution of sociality. Although spiders are not insects, one behavior is not limited to one species. There are many social and eusocial insects, birds and mammals. Can spiders cross over from asocial to social beings? If so, does it really benefit them in any way?

There are advantages to becoming a social spider, reduced energy in silk production when web building, protection from predators and aid in maternal care. However, in order to become social, one must also become tolerant of conspecifics; this is true throughout species and among individuals of a species. With that tolerance comes a loss of aggression toward predators, decrease in activity, and less interest in superfluous prey capture. Caste systems will develop through competition for food and other resources, inbreeding increases which is a bad thing in general, although it hasn't been shown to be a negative thing in this case yet. Ecological niches are filled with the organism that can adapt the most effectively. Spiders are adapting quite well to niches at multiple levels and it appears we will continue to observe them at both the social and asocial level for some time.