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Social behaviour by captive juvenile *Kukulcania hibernalis* (Araneae: Filistatidae)

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Summary

This paper describes the interactions of captive *Kukulcania hibernalis* spiderlings both among themselves and with regard to the maternal females. We found that, at least through the third post-emergence instar, *K. hibernalis* spiderlings display behaviours consistent with the criteria outlined by Kullmann (1972) for a spider to be considered a social species: tolerance, aggregation, and co-operation. Spiderlings were observed daily from emergence through the third post-emergence instar and were seen to exhibit sibling recognition, co-operative prey capture and feeding, and formation of aggregations both after feeding and after dispersal from the maternal web. No spiderlings were observed to feed with the mother and there appeared to be no consistent provisioning for the spiderlings by the mother. These results represent the first example of social behaviour by a filistatid species and extend the taxonomic range of social behaviour in araneomorph spiders.

Introduction

Spiders usually are considered to be non-social predators. Cannibalism is a common source of mortality in some species and in many species special behaviours are necessary for males to approach females safely for mating. Nonetheless, some level of sociality has been documented in at least 17 spider families (Buskirk, 1981; Aviles, 1997) and it is considered to be of polyphyletic origin (Kullmann, 1972). Social behaviour in spiders is postulated to have evolved along either of two pathways. The "sub-social pathway" is thought to be an extension of maternal-juvenile and sibling tolerance into adulthood (Kullmann, 1972). In contrast, the "para-social route" is thought to occur through decreased aggression in response to favourable environmental circumstances (e.g. Uetz & Hodge, 1990).

To study the evolution of sociality in spiders, one strategy is to examine species that display less advanced forms of social behaviour for clues as to the ancestral condition. Papers by Shear (1970) and Kullmann (1972) stimulated searches for intermediate forms of sociality in spiders over the past two decades, resulting in an increase in the number of families known to include social species. Kullmann (1972) listed three attributes that must be present for a spider species to be considered as social: individuals must tolerate the presence of conspecifics, there must be an "urge to aggregate", and individuals must show some form of co-operation. Here we report, what is to our knowledge, the first example of social behaviour in the Filistatidae. We found that, when juvenile, *Kukulcania hibernalis* (Hentz) displays behaviours consistent with Kullmann's criteria. In addition, we describe the behavioural interactions of the maternal female with her offspring.

General biology

The Filistatidae comprises 15 genera that are world-wide tropical to warm-temperate in distribution (Platnick, 1997). They generally are considered to be primitive spiders (Zonshtein, 1990), although Lehtinen (1967) suggested that they are rather advanced in some characters. *Kukulcania hibernalis* often can be found in large numbers in the southeastern United States (Edwards, 1983). This relatively large species constructs webs in cracks and crevices, often on and in buildings, emerging from a tube-like retreat to capture prey trapped in cribellate webs (Deyrup *et al.*, 1988). In addition to constructing their own webs, individuals of this species will readily occupy empty webs (Deyrup *et al.*, 1988).

Adult *K. hibernalis* are typically solitary and display extreme sexual dimorphism (Edwards, 1983). Females may live for several years after reaching sexual maturity (Edwards, 1983) but adult males are relatively short-lived. The exact time after mating when egg sac production occurs has apparently not been reported. In our laboratory, females produced egg sacs after as long as six months of isolation, so sperm storage may be possible in this species. In captivity, the female typically attached the egg sac to the wall of her retreat and remained with it throughout the incubation period. Egg sac production was not observed, so it is unknown whether the egg sacs were constructed in place or moved to the retreat after completion. The onset of emergence of the spiderlings also was not observed, so it is not known whether the female assisted in opening the egg sac.

Material and methods

Adult *K. hibernalis* were captured on buildings at the Archbold Biological Station (Fla, USA) in February and transported to the University of Missouri. Spiders were maintained individually in plastic boxes (5 × 7 × 12 cm) in the laboratory at ambient temperature (21–24°C), with 12:12 light:dark cycle. The spiders were fed mealworms (*Tenebrio* sp. larvae) 2–3 times/week. Water was supplied at feeding by misting the interior of the cage or by placing a few drops of water on a sponge placed inside the cage.

Five field-collected females subsequently produced egg sacs and the embryos were allowed to develop *in situ*. After emergence, spiderlings were maintained in their natal cages with the females. Since we wished to observe behaviours with as little disturbance as possible, we did not measure the spiderlings at emergence. Daily observations by eye or with the aid of a dissecting microscope were continued for eight weeks through the third post-emergence instar. Particular attention was paid to feeding behaviour by the spiderlings. Three weeks after the emergence of the spiderlings, the natal cages were placed without lids inside larger plastic containers (21 × 31 × 11 cm) to allow room for possible dispersal of spiderlings.

After emergence of the spiderlings, we continued to provide the adult females with mealworms 2–3 times per week. In addition, 10–20 fruit flies (*Drosophila melanogaster*) were dropped on to each web 2–3 times each week. Fruit flies and mealworms were never added on the same day. Fruit flies that escaped the web were allowed to remain in the cages. During the last five weeks, a culture vial containing fruit flies was kept in the cage to provide *ad libitum* access to food for any dispersing individuals. At the end of the observation phase, all cages were closely examined for spiderling carcasses or evidence of cannibalism. Also at this point, two of the egg sacs were opened and examined for unemerged spiderlings and exuviae.

In addition to general observations, the behaviour of female *K. hibernalis* in the presence of fruit flies was examined. Twelve non-maternal adult females on the same mealworm-feeding schedule as the maternal females were presented with 10–20 fruit flies in the same fashion as were females with spiderlings. The non-maternal spiders then were observed for 15 min to ascertain whether they consumed fruit flies.

Results

Female behaviour

Over the course of several weeks, adult female *K. hibernalis* produced a loosely organised web of cribellate silk extending from an open-ended tube which the female used as a retreat and within which the maternal females placed their egg sacs. Except when feeding, females maintained contact with the egg sac throughout the incubation period.

Maternal females fed regularly, both throughout the incubation period and after the spiderlings emerged. Mealworms were attacked shortly after they were placed on the web. Females wrapped the prey using alternating movements of legs IV before biting. Prey consumption occurred at the point of capture. Under the same conditions additional females (several hundred feedings involving >50 individuals) also consumed prey where they were captured. A single instance of prey being moved was observed when one of the maternal females wrapped and immobilised a mealworm but did not consume it. Instead, the female carried the mealworm in her chelicerae to an area near where the spiderlings were aggregated. This was the only time spiderlings (as many as six) were observed feeding on a mealworm. There was no evidence of food storage as no prey item was wrapped but left unconsumed, although in one instance a maternal female approached several fruit flies on the web and touched the flies with both pedipalps in an alternating fashion, resulting in the flies being pushed farther into the web. These flies were subsequently ignored by the female.

Maternal females were never observed consuming fruit flies. When 12 non-maternal females were presented with fruit flies, four of them consumed one or more of the flies within 15 min. The spiders attacked flies differently than they did mealworms. After locating the prey, a spider grasped the fly with her chelicerae, pulled the fly from the web, and consumed it directly without wrapping.

Maternal females appeared actively to discourage contact by their spiderlings. When spiderlings attempted to climb on to a leg of the mother, she rapidly flicked that leg, which resulted in the spiderling altering its direction and moving around the female. This behaviour was observed repeatedly and typically occurred while the spiderlings were being fed. All five maternal females moulted after producing an egg sac. No additional egg sacs were produced, although all females survived for at least ten months after the first egg sac was produced.

Spiderling behaviour

Spiderlings began to emerge 76 ± 4 (mean $\pm$ SE, $n=5$ egg sacs) days after oviposition. Emergence occurred over a period of approximately 36 h and was preceded by an enlargement and thinning of the egg sac that lasted 2–3 days. All siblings emerged through a single hole in an egg sac. In one case, the hole was located such that spiderlings remaining in the egg sac could be observed. Considerable movement of the spiderlings was evident within the egg sac and individuals seen near the exit hole often retreated back into the mass of spiderlings. After emergence no spiderlings were seen to re-enter the egg sac.

The mean number of spiderlings recovered at the end of the observation phase was 81 ± 14 (mean $\pm$ SE, $n=5$ groups). Examination of the cages after removal of the spiderlings revealed at most a few (1–2) spiderling carcasses. Egg sacs contained numerous exuviae, all of which were of similar size. One egg sac also contained four dead spiderlings.

After emergence, spiderlings remained in a tightly clustered group within the female's retreat, often occupying opposite sides of the same spot on the web. Although all spiderlings appeared to maintain contact with the web, it was not uncommon for an individual to have one or more legs on, or in contact with, other spiderlings. After the first week, spiderlings dispersed during prey capture and consumption, but then reformed their aggregation. After the first two weeks, the aggregation was not always in the female's retreat, rather, the location varied from day to day. Spiderlings that extended their movements beyond the natal cage after it was placed in the larger container typically formed small tightly-clustered groups of 6–10 spiderlings.

Differentiation of sibling from prey appeared to occur through contact. When spiderlings encountered one another on the web, both individuals typically raised both legs I. After briefly touching the other spider's legs, spiderlings altered their paths to pass each other. In most cases two or more spiderlings were involved in wrapping a prey item in silk at the same time. This behaviour appeared to require physical contact with the prey, as spiderlings on the periphery did not exhibit this behaviour until contact was made with the insect. Prey wrapping behaviour by the juveniles was similar to that of the adults.

Most spiderlings fed communally until eight weeks after emergence. Typically two or more spiderlings fed

on the same fly. There did not appear to be any segregation by individuals of different instars when multiple instars were present simultaneously. The composition of a group of feeding spiderlings appeared to be dynamic: spiderlings often moved from one feeding group to another before a fruit fly was consumed. Such movement did not seem to be the result of aggression by other spiderlings, but rather by casual displacement, since a single fly could only support six to eight feeding spiderlings. Some entrapped flies on the web remained uneaten when spiderlings returned to the maternal retreat. There was no apparent evidence of active recruitment of spiderlings in subduing prey, although the actions of one spider often seemed to attract others. At the same time, there were no apparent attempts to monopolise a prey item. Although most spiderlings fed communally, spiderlings were not observed feeding on a prey item with the mother. Solitary first post-emergence instar spiderlings were capable of capturing and consuming a fruit fly. In one case the entire process was observed. In this instance the spiderling sucked out the contents of the head and thorax of the fly through the head, then repositioned itself and repeated the process through the abdomen of the fly. This process required nearly two hours from initial contact to completion of sucking out the fly. In contrast, when several spiderlings fed on the same fly, the process took about 10 minutes.

Spiderlings added silk to the maternal web, and those that left the natal cage extended the web beyond its original dimensions. Juveniles also appeared to be capable of using the properties of the web in locating prey. Spiderlings typically took a rather linear route from the retreat, and attacked the first fly encountered provided there was room for access. There was a general tendency to feed first on flies that were closest to the retreat, while flies farther from the retreat were consumed later. Adult *K. hibernalis* used a stop-and-go approach to trapped prey, first moving forward and then stopping and testing strands of webbing, apparently to ascertain in which direction to proceed, before reorienting and moving farther. The spiderlings were observed to behave in a similar manner when approaching a fruit fly, often from a distance of 3–4 cm. Responses to the appearance of prey on the web were very rapid; typically some of the spiderlings were moving out on to the web within 30 s after flies were placed on the web.

The first evidence of moulting by spiderlings occurred approximately four weeks after emergence. Spiderlings in their second post-emergent instar were about twice as large as their siblings that had not yet moulted, had a more adult-female-like shape, and no longer had a translucent carapace.

Discussion

Maternal behaviour

Females of many spider species exhibit some degree of parental care (Kullmann, 1972). Female *K. hibernalis* maintained contact with the egg sac during incubation except when feeding. After emergence of the spiderlings,

there appeared to be little change in the general behaviour of the females. Females continued to feed normally and all females moulted. This is in contrast to females of other species that cease feeding after egg-laying or after emergence of the young although they may survive to provide protection for the spiderlings. Further, it is known that female K. hibernalis can live for several years after sexual maturity (Edwards, 1983), thus survival of the female is not simply to serve as a food cache for her spiderlings (Kullmann, 1972).

Several spider species have evolved behaviours by which the females provide their offspring with food (Shear, 1970), from providing captured prey (Brach, 1976; Gundermann et al., 1988) to regurgitation of special secretions by the female (Kullmann, 1972). Provisioning behaviour was observed only once in this study; however, under natural conditions this behaviour may be more prevalent. Maternal behaviour in some spiders is known to be affected by the presence or behaviour of offspring (Gundermann et al., 1988; Roland et al., 1996). It is possible that frequent feedings prevented the spiderlings from displaying behaviours that would elicit provisioning behaviour by the female. There was no evidence of female provisioning through regurgitation as has been seen in some spider species (e.g. Kullmann, 1972). Maternal females did not participate in communal feeding with the spiderlings. This may represent some type of "niche separation" whereby adults and juveniles feed on distinct size classes of prey. This may account for the apparent "breakdown" of tolerance that leads to the solitary existence displayed by adults. The mother may tolerate the offspring until they become large enough to compete for the same prey (Seibt & Wickler, 1988). In this way she may gain fitness advantages by providing protection (Gundermann et al., 1997) and, by allowing the use of her web, more food for her offspring at little cost to herself when the spiderlings are small (Jakob, 1991). Alternatively, the aggregation may remain intact as long as the food supply is sufficient to provide for both the mother and the spiderlings (Smith, 1983); only when the food supply is depleted do the spiderlings disperse.

Females appeared to tolerate the presence of spiderlings in their retreats, but they actively avoided direct contact with their offspring. In contrast, wolf spiders (Eason, 1964) carry their offspring on their bodies. This difference may reflect the hunting styles of the species. Wolf spiders are active hunters that do not remain in one place whereas K. hibernalis is a sit-and-wait hunter and does not leave its web.

There was no evidence of cannibalism of the offspring by the female. One possible explanation for this observation is that the spiderlings were too small to provide enough nutrient return. Since maternal females also did not appear to pay any attention to fruit flies, which were of similar size to the spiderlings, this possibility cannot be discounted. However, some non-maternal females were seen to consume fruit flies, suggesting that fruit flies (and by implication, the spiderlings) are not physically too small to become prey for adult females. A second explanation for the lack of response to the fruit flies is that an inhibition of consumption of small prey exists when spiderlings are present. Finally, the frequent feeding of females may have allowed them to be more selective. High prey levels are known to reduce cannibalism in spiders (Rypstra, 1986). Most non-maternal females did not consume fruit flies, suggesting that the level of feeding may have contributed to the lack of response by the maternal females to fruit flies.

Spiderling behaviour

Through the third post-emergence instar, juvenile K. hibernalis were typically found in close proximity to each other without signs of aggression, thus this species can be considered a "contact species" (Burgess, 1978). Even after leaving the natal cage the spiderlings typically reformed aggregations after dispersing to feed. The locations of these aggregations varied and there was no apparent pattern in terms of structure (e.g. corners, natal cage, etc.), suggesting that the spiderlings were not returning to a specific spot, but were in some way attracted to areas containing other spiderlings. The young of many species remain together briefly after emergence; however during this period many do not feed actively (Buskirk, 1981). The period of tolerance may end with the onset of feeding or after a specific developmental stage is reached (Krafft, 1975). The spiderlings in the present study displayed tolerance after the onset of feeding that persisted into at least the third post-emergence instar. It is possible that frequent feeding promoted the longevity of sibling aggregations, since tolerance of the presence of other spiders is affected by food availability (Rypstra, 1983, 1989; Uetz & Cangialosi, 1986) and increased food supplies can allow siblings of some species to remain together longer (e.g. Krafft et al., 1986).

Differentiation of sibling from prey appeared to occur through contact in K. hibernalis juveniles by a recognition sequence involving contact using legs I. Similar behaviour has been seen in other social species (Kullmann, 1972; Bessekon, 1997) and is consistent with Foelix's (1970) observation of chemosensory hairs on the tarsi of filistatids. Brach (1976) suggested that "surface-specific recognition" in some of the more advanced "quasisocial" spiders was related to communal prey handling and acted to control intraspecific aggression during prey capture. The ability to differentiate sibling from prey was not limited to specific instars. After the onset of moulting, it was common for individuals of different instars to feed on the same prey item.

Communal feeding by K. hibernalis spiderlings did not seem to be the result of limited prey. In all cases, although the number of fruit flies was less than the number of spiderlings, spiderlings stopped feeding before all of the fruit flies were consumed. Spiderlings were never seen to attack a mealworm, either alone or in concert as might be expected if communal behaviour evolved in response to the need to capture larger prey. It is possible that the mealworms exceeded some maximum size that prevented an attempt at capture by the spiderlings.

Juveniles consumed prey at the point of capture, which was typically away from the retreat. Solitary juveniles took much longer to finish feeding than did spiderlings in groups. One possible advantage of communal feeding is that it reduces the amount of time an individual is exposed to predation. Thus, communal feeding may allow more spiderlings to gain sufficient food in a shorter period of time, thereby reducing exposure away from the maternal retreat.

Another advantage is that the combined efforts of several spiderlings working on different portions of the prey item may digest the prey more efficiently. Krafft (1965) showed that the digestive juices of social spiders mix during communal feeding, and D'Andrea (1987) suggested that the mixing of digestive juices from multiple individuals may enhance the processing of prey. It is likely that different parts of a prey item contain different proportions of various nutrients; thus when several spiderlings digest the various parts of the prey at once, mixing of digestive juices may occur, providing each spiderling with access to all soluble components, and a more balanced diet, more quickly. This may have important fitness consequences since diet composition is known to affect growth rate, time to maturity, and longevity (Lowrie, 1987).

Webs are a common feature in most social spiders (Aviles, 1997) and juveniles appeared to use the properties of the web quite efficiently. Spiderlings were seen to add silk to the maternal web and, among spiderlings that left the natal cage, to extend the boundaries of the maternal web. Juveniles may not be capable of producing individually a web large enough to provide a sufficient prey base. Remaining on, or adding to, the mother's web may be an adaptation to allow sufficient foraging area for the spiderlings until they are capable of constructing an adequately sized web for themselves. Further, remaining on the mother's web may provide an economy of silk usage (Riechert, 1985), allowing more allocation of energy to growth. Finally, the spiderlings may be incapable of producing an effective web of their own. It is known that early instars of some cribellate species lack a fully developed cribellum (Szlep, 1961). To our knowledge this possibility has not been examined in *K. hibernalis*; however, if this species lacks a functional cribellum in early instars, remaining on the mother's web may allow greater access to food during this period.

General discussion

This report represents, to our knowledge, the first evidence of social behaviour by a filistatid species and the second report of sociality in a haplogyne spider. Through at least the third post-emergence instar, juvenile *K. hibernalis* display behaviours consistent with the criteria outlined by Kullmann (1972) as necessary for a spider species to be considered as social: tolerance, interaction, and co-operation.

Social behaviour among spiders can be assigned to one of four categories depending upon whether or not the species displays territoriality and whether or not the associations are permanent (D'Andrea, 1987).

K. hibernalis could be considered sub-social (Wilson, 1971), or, more specifically, non-territorial periodic social (Aviles, 1997), since the communal behaviours of the juveniles and the tolerance by the mother apparently break down later in development. Assuming that the number of spiderlings recovered is a reasonable estimate of egg production in this species, the number of offspring is near the range proposed by Kullmann (1972) for sub-social species. Selection for retention of tolerance by the mother for the presence of the offspring and by the juveniles for each other could produce a permanent social structure (Buskirk, 1981; Kullmann, 1968).

K. hibernalis occurs in a region where seasonality is reduced, as is the case with most group-living spiders (Aviles, 1997). Although there is no simple relationship between seasonality and sociality (Buskirk, 1981), as a sub-tropical species *K. hibernalis* may not be subjected to environmental limitations on overlap of generations that more temperate species must endure. Females of this species are known to live for several years. The fact that the female does not die after the spiderlings emerge can be loosely interpreted as an overlap of generations, and extension of the tolerance period could rapidly lead to true overlap of generations. One might speculate that this is the same route as was taken by *Diaea* species (e.g. Main, 1988) in which new colonies are formed by a single female and her offspring. In these species siblings continue to exhibit co-operative behaviour after sexual maturity. In fact, the expansion of the core web of the mother by the juveniles seen in this study was similar to that reported for the *Diaea* species.

Shear (1970) suggested looking for "pre-adaptations" that may lead to sociality in spiders. Communal feeding alone does not constitute sociality. Co-operative capture behaviour by the young of solitary adults occurs in various spider species, and co-operative food procurement and feeding are not universal among spiders that live in groups (Buskirk, 1981). In *K. hibernalis* however, communal feeding is accompanied by an apparent "urge to aggregate", extended tolerance both by the mother for the offspring and by the spiderlings for each other, a well-developed mechanism for differentiating sibling from prey, upkeep and extension of the maternal web by the spiderlings, and a willingness by adult females to accept the webs of conspecifics. Any or all of these behaviours could be regarded as preadaptations to social behaviour. The existence of these behaviours in a relatively primitive family may provide clues to the evolution of sociality in spiders.

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