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Note added in proof

After this paper had gone to press, we received some further information about continental records of *M. fuscipalpa* from Theo Blick and Herman Vanuytven (in litt.) referring to papers by Blick (1999) and Vanuytven (1992) respectively. In Germany the species is listed as occurring mainly in grassland on sandy disturbed ground, and sometimes on sandy arable land and intensively grazed pasture. In Belgium it was found among grass on a dyke and on open sandy ground near a road and a wood. This is in general agreement with the habitat in Suffolk.

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Sub-social behaviour in the diplurid *Ischnothele caudata* (Araneae, Dipluridae)

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Summary

Investigations of the behaviour of *Ischnothele caudata* (Araneae, Dipluridae) in the laboratory have shown this species to exhibit sub-social behaviour, an as yet unreported phenomenon in orthognath spiders. The females care for their young after hatching by providing food. Experiments showed the care by the mother to be necessary for the spiderlings during a critical phase of at least 5 weeks, with the young gaining weight faster and having higher chances of survival.

Introduction

Spiders have always been regarded as a typically solitary animal group, even though several dozen species from at least 9 different families have evolved living in groups (Shear, 1970; Kullmann, 1972; Buskirk, 1981; Uetz & Hieber, 1997; Aviles, 1997). Authors are largely agreed on the evolutionary process that led to social behaviour in Araneae. Two different processes have been discovered. One led from an aggregation of adult animals under certain environmental conditions to a way of life that resembles more a mutual tolerance than co-operation. This evolutionary path, which is mostly postulated for orb-weaving spiders, occurred while the spiders retained their solitary way of life. No co-operation takes place, but merely a reduction of the distance between the webs to a minimum (Burgess, 1978; Krafft, 1982a, b; Uetz & Hieber, 1997). The other process, most likely involved in the evolution of social behaviour in the non-orb-weaving species, has its origin in the caring for offspring, which was expanded temporally until spiderlings stay with their mother for life. In the highest evolved species this leads to co-operation in all aspects of life (Burgess, 1978; Krafft, 1982a, b; Lubin, 1995; Aviles, 1997).

All authors agree, furthermore, that two things are necessary as pre-adaptations for social behaviour: a web as a medium of information transfer, and life in the tropics or sub-tropics where potential prey is abundant year-round (Nentwig, 1985).

Social behaviour in spiders has only been known in the labidognaths, the more modern, more highly developed group, but has never been observed in the orthognath spiders (Shear, 1970; Aviles, 1997). Darchen's report (1967) on a social diplurid, *Macrothele darcheni* Benoit, has to be viewed with a certain amount of scepticism, as he was only able to study a single web and did not conduct any behavioural experiments. Galiano (1972) gave a detailed description of the development of *Ischnothele siemensi* F.O.P.-Cambridge (=*I. guianensis* (Walckenaer)) and observed that third instar spiderlings remain for varying periods in the maternal web, where they may capture small prey and then disperse to construct their own webs. Paz (1988) observed no social behaviour in any form in a study on a species of *Linothele* (Araneae, Dipluridae) in which residents treat conspecific intruders into their webs as prey. Coyle (1995) in his revision of the subfamily Ischnothelinae gives no further reference to social interactions in *Ischnothele*, but mentions observations suggesting that older juveniles of the African species *Thelechoris striatipes* (Simon) sometimes remain in the maternal web for extended periods. Although these are

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only anecdotal observations, we assume that diplurids are ideal for a study on sociality because they are pre-adapted for the evolution of such behaviour by building semi-permanent webs and living in the tropics. Additionally, many species live in stable habitats and typically reside for many months in a given web.

During ecological field and laboratory studies on the diplurid *Ischnothele caudata* Ausserer, we observed females providing their young with food by catching prey for them. This study attempts to ascertain whether *I. caudata* shows additional social responses by investigating care of the young and other expressions of social behaviour.

Material and methods

Ischnothele caudata is found from the Yucatan Peninsula south and east through Central America and throughout northern South America north of the Amazon Basin and east into the Lesser Antilles (Coyle, 1995). They build webs in small holes on the ground, between fallen branches, among litter or on structured palm trunks. Webs are approximately 30 cm in length and width, relatively unstructured and include a funnel as retreat. Webs can be either small and rather inconspicuous or reach large sizes, e.g. when a colony covers a palm trunk over a length of several metres. In larger webs the retreat funnel may have several entrances and in colonies the retreats may have connecting tubes.

Mature females are approximately 1.5 cm in length. Males are marginally smaller and narrower. The animals used in the study were caught in the wild in Panama (Pipeline Road, Gamboa, Parque National Soberanía) where this species is locally abundant (Nentwig, 1993). In the laboratory the spiders were kept in opaque plastic boxes (18.3 × 13.6 × 4.3 cm) with transparent lids under constant conditions (25°C, 14L:10D). The bottoms of the boxes were covered with plaster to ensure sufficient humidity. Rearing in captivity is rather easy, since this species has no defined breeding season and offspring are produced throughout the year. The spiders were fed twice a week with *Drosophila melanogaster*, *Acheta domesticus*, *Calliphora erythrocephala* or *Musca domestica*, according to their size. Our laboratory stock persisted for more than 6 years.

Cocoon defence was investigated on 25 females by disturbing the animals with increasing intensity: lightly nudging the box, removing the lid of the box, plucking on the web, and touching the spider. Their reactions (settling on top of the cocoon, staying close to the cocoon, nervously running back and forth, fleeing into the dwelling tube) were recorded. The behaviour of the female was recorded with a video camera at the time of hatching of her young. The behaviour of adult females, adult males and subadult females was observed during feeding with spiderlings present.

Recognition of young by *I. caudata* was studied by placing spiderlings of either another female of the same species or of *Argiope argentata* (Fabricius) (Araneidae) or *Cupiennius salei* (Keyserling) (Ctenidae) into webs of females where the young or the cocoon had been removed. Food-providing behaviour by females for young not their own was measured by weighing the spiderlings placed in their webs and comparing their weight with control young left with their mother.

The effect of care by the mother on her offspring's weight was studied by removing the spiderlings from their mother's box two days after hatching and placing them in separate boxes in groups of 1, 2, 10, 20 and 50. Fifty spiderlings were left with each mother. Each group was weighed once per week (Sartorius fine balance, type 1405). The number of individuals in each group was counted twice a week and dead animals and moultings were recorded.

The effect of the length of time the female of *I. caudata* cares for its young was measured by removing the spiderlings from their mother's box after 1, 2, 3, 4 or 5 weeks and placing them in pairs in boxes of their own.

Owing to misidentification of *I. caudata* as *I. guyanensis* some previous publications on *I. guyanensis* (or *I. guianensis*) refer to *I. caudata*. This concerns the study of Nentwig & Wissel (1986) on predator-prey length relations, Strohmenger & Nentwig (1987) on silk production, and Jantschke & Nentwig (1987) on feeding behaviour. A recent taxonomic revision of this genus and a complete bibliography has been given by Coyle (1995).

Results

Females build a large, flat, lens-shaped cocoon 12.5 ± 3.2 ($n=31$) days after copulation. The cocoon is guarded by the female until the young hatch after 17.0 ± 1.1 ($n=27$) days. Depending on the extent of disturbance or threat to the cocoon, the female stays close to it or disappears into the nearest silk funnel, e.g. when the female herself is touched or if the web is damaged (Table 1). The average number of young hatching from one cocoon is about 300. Up to 5 cocoons

Type of disturbance	Settling on top of cocoon	Staying close to cocoon	Nervously running back and forth	Fleeing into dwelling tube	No reaction
Nudging the box	19	5	0	0	1
Removing the lid	12	4	2	3	4
Plucking on the web	10	3	1	8	3
Touching the animal	2	5	1	13	4

Table 1: Reactions of females with cocoons to disturbances of varying intensity ($n=25$).

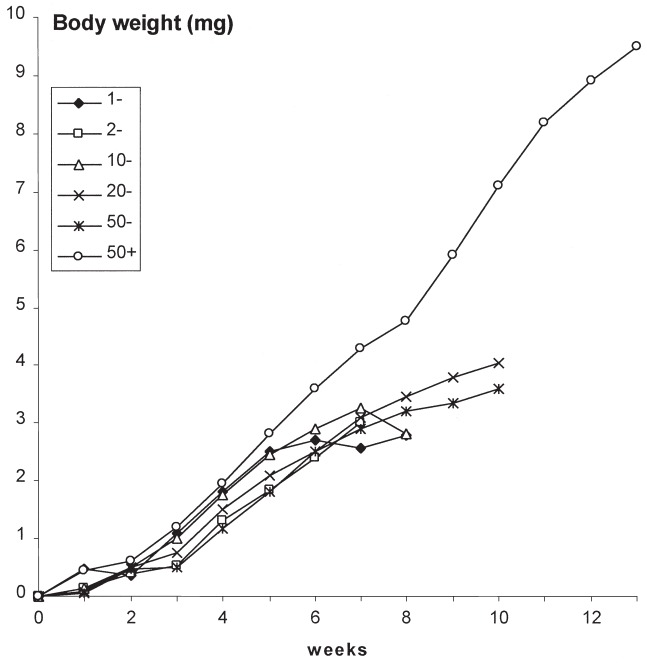

Fig. 1: Weight gain of spiderlings kept in groups of different sizes (1, 2, 10, 20, 50) with (+) or without (−) their mother. Number of groups=45 (1−); 37 (2−); 40 (10−); 38 (20−); 32 (50−); 15 (50+).

were built after one copulation, but never more than 4 contained fertile eggs.

Shortly before the young hatch, the female begins nervously walking back and forth, stopping to sit on or beneath the cocoon for short periods. In order to help the spiderlings hatch, the female plucks on the cocoon with her pedipalps and chelicerae. The young hatch over several hours and spread out over the web within a few days after hatching. The mother's help does not seem to be necessary during hatching, however, as the young hatch without a discernibly higher mortality when no female is present.

The female feeds her young by catching large prey (e.g. *A. domesticus*) and killing and placing it on the web. Smaller prey, e.g. *D. melanogaster*, are caught one after another and pressed together with the chelicerae. These "parcels" are deposited in different places on the web. In both cases the female begins to scurry back and forth afterwards, spinning on the web at the same time. When the brood is young, the mother attracts the spiderlings by plucking on the web with all eight legs simultaneously and by beating on it with her pedipalps. Within one to two minutes all the spiderlings find the prey and feed together. The young spiders react to and catch smaller prey on their own after a few days. *Ischnothele caudata* does not eat carrion and therefore does not react to long-dead prey in the web. Not even young spiderlings without their mother ate dead *A. domesticus* which were placed in the web, but they accepted freshly dead flies when they had been killed by the female. This may also explain the bad performance of individually raised spiderlings (Fig. 1). Older spiderlings react immediately to the vibrations caused by prey or run immediately to the mother after prey-capture and begin feeding while the insect is still in her chelicerae.

The trigger for the feeding behaviour by the mother is the presence of spiderlings on the web. Females without young do not show this provisioning and signalling behaviour even after copulation or when they have built a cocoon. Feeding behaviour can be induced, however, by placing spiderlings in the web of a female that has copulated. Subadult spiders and males do not feed young actively. However, they tolerate juvenile spiders feeding on their prey or surrender it altogether when not hungry themselves.

There was no difference between the weight of young raised by females not their mother and young raised by their own mother. Spiderlings of species other than *I. caudata* (*A. argentata* and *C. salei*) were captured and eaten ($n=10$ each).

As shown in Fig. 1, spiderlings raised in groups with their mother gained weight considerably faster after 5 weeks than the spiderlings in the other groups. Even spiderlings kept singly showed comparable weight gain in the first 4 weeks. Mortality was higher in the groups without their mother after 6 weeks (Fig. 2). The beginning of the increased mortality rates is correlated with the third and fourth moult after hatching, and none of the spiderlings raised without their mother survived the eleventh week.

Mortality in spiderlings removed from their mothers decreased with the length of time they were allowed to spend in their mother's box before removal (Fig. 3). Spiderlings that were removed after 1 to 3 weeks became apathetic around the time of the second moult, stopped reacting to prey and died during the next moult. Spiderlings removed after 4 weeks showed similar reactions, although delayed by several weeks; mortality occurred at a more advanced age and some animals survived. Only when the animals were left with their

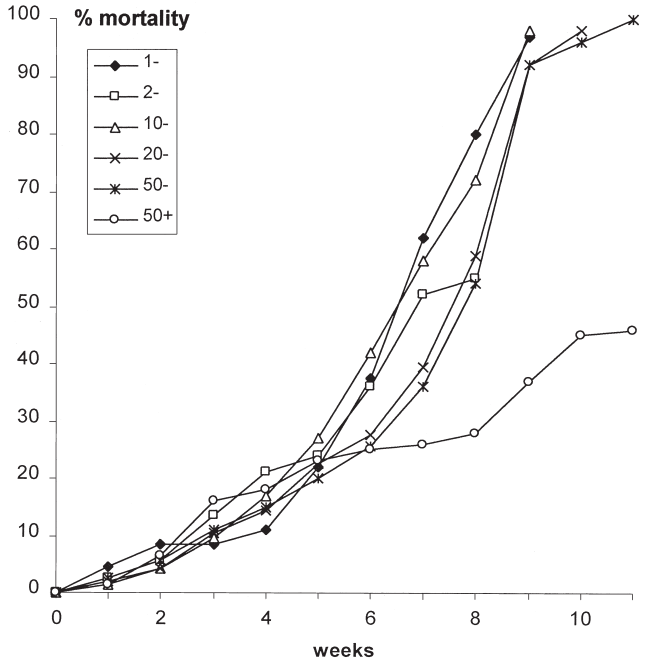

Fig. 2: Cumulative mortality of spiderlings kept in groups of different sizes (1, 2, 10, 20, 50) with (+) or without (−) their mother. Number of groups=45 (1−); 37 (2−); 40 (10−); 38 (20−); 32 (50−); 15 (50+).

mother for 5 weeks before removal did the mortality rate remain below 80%.

Although spiderlings only 3–5 days old are capable of catching *D. melanogaster* by themselves, they usually co-operate and then feed simultaneously, even tolerating spiders that have not co-operated in catching the prey. This behaviour disappears after the first moult, except when catching larger prey, when it could be observed until the spiders were 18 weeks old.

Cannibalism of young by the mother was never observed. On two occasions medium-sized young attacked and ate their mother shortly after she had moulted. The spiderlings are usually very hungry at this point because the mother does not feed them for up to a week before moulting. Sometimes the spiderlings ate other, freshly moulted spiderlings. Only during 3 of 58 observed copulations was the male eaten by the female.

Males usually stay in the webs of females for several weeks, even after a cocoon has already been built or the young have hatched. In captivity, up to 3 females may stay together in one large web, build their cocoons and feed their young. The females either end up in the same web because a female invades a web that is already occupied and is tolerated or because web enlargement leads to overlaps, thus sometimes forming large colonies. In such cases the females do not restrict their activity to their own webs but are found in all parts of the joint web. When two females approach prey, however, one—not necessarily the smaller individual or the original owner of the web—always retreats. Young that leave their mother's web may either stay in another female's web or build their own web, in which several spiderlings usually live together. New spiders that were added to a box usually stayed in the web where they were placed, irrespective of whether the web was occupied or not. Owners moved towards the intruders when they were placed on the web, but retreated before contact or released the intruder immediately after attack without inflicting injuries.

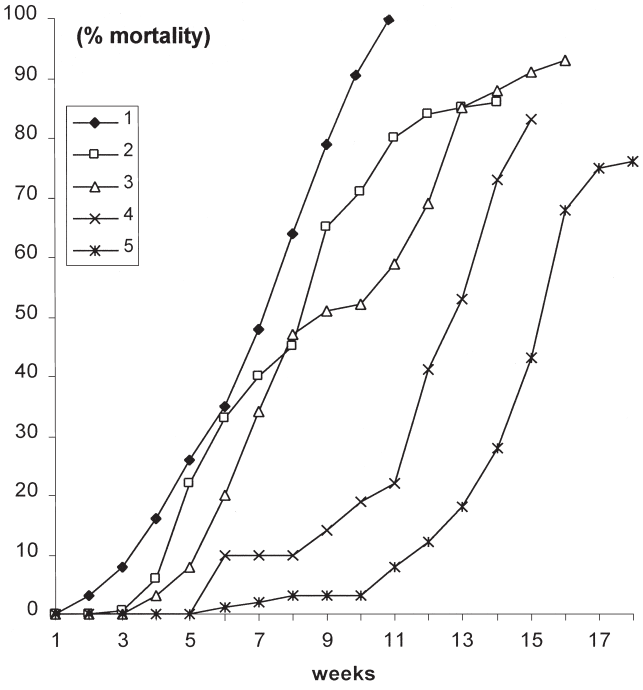

Fig. 3: Cumulative mortality of spiderlings removed from their mothers' boxes after varying periods of time (1, 2, 3, 4, 5 weeks). Number of individuals = 86 (1); 98 (2); 71 (3); 49 (4); 72 (5).

Discussion

Ischnothele caudata defends its cocoons against minor disturbances. It makes sense for the mother to protect her cocoon from rain or wind or egg parasites, e.g. parasitic wasps. When attacked by predators that are dangerous to the spider itself, however, the spider fares better if it gives up the cocoon and protects itself. Accordingly, *I. caudata* retreats when confronted with stronger disturbances or when touched.

The mother has also been observed assisting the young in hatching in other spider species, e.g. *Stegodyphus sarasinorum* Karsch (Eresidae) (Jacson & Joseph, 1973; Krafft, 1982a), lycosids (Foelix, 1992) and *Cupiennius salei* (Ctenidae) (Melchers, 1963). These are mostly species that guard their cocoon, like *I. caudata*. Assistance in hatching, however, is not necessarily a step towards the evolution of social behaviour. For example, *C. salei* is a solitary non-web-building species and no social behaviour has been observed in the Ctenidae. Almost all the lycosids lack the web as a necessary pre-adaptation for the development of social behaviour. On the other hand, the opening of the cocoon by the mother has not been described for many social species.

The different experiments have shown that *I. caudata* has developed a social behaviour. The females care for their young over the course of several weeks by providing food. The advantages to the young are evident in the faster weight gain and lower mortality compared with young that were raised without their mothers. The care by the mother seems to be necessary for the spiderlings, at least for a certain time. The spiderlings tolerate each other in their mother's web over a long period of time. Tolerance for other *I. caudata* of all age groups is also pronounced among adults, while spiders of other species are recognised as prey.

To investigate whether the social behaviour reported here was influenced by the laboratory situation, we placed some spiders in a 70 × 120 cm large arena or allowed them to build their webs in palm trees in a glasshouse of our botanical garden. In both situations the spiders did not distribute their webs regularly within the available space, but always built their webs attached to each other. We observed males and females or two females for several days in the same web. The mother fed her offspring in the same manner as described above and joint hunting and feeding could also be observed among groups of juvenile spiders. The main elements of the behaviour described here were also observed under natural conditions in Panama, especially coherent web colonies where individual webs housed several spiders. We also observed several spiders feeding on one prey item in Panama.

The providing of food for the young by the female has been observed in other species, e.g. *Coelotes terrestris* (Wider) (Amaurobiidae), and is thought to influence the

cohesion in spider colonies (Krafft *et al.*, 1986). Another way to provide the young with food is regurgitation, which has been observed in various families (e.g. Brach, 1977).

Males of *I. caudata* often stay in webs of different females, while the occupation of one web by several females is probably more the exception than the rule, although they, too, are tolerant of each other. Young that have left their mother's web either stay in webs of other females or in webs of other spiderlings. Cannibalism occurs only rarely and may perhaps have been provoked by the laboratory situation. This high level of tolerance is not an inevitable consequence of colony-building, as was shown in *Eriophora bistriata* (Rengger) (Araneae, Araneidae), where individuals do not tolerate others on their webs even though they are built close together and interlinked (Fowler, 1978).

Based on these findings *I. caudata* can be classified as exhibiting a periodic-social behaviour as defined by Kullmann (1972) or subsocial as defined by Wilson (1971). The evolution of social behaviour seems to have set in early in spiders, i.e. with the orthognaths. Among the orthognaths, the diplurids, with their long-lived webs, seem to be pre-adapted for the evolution of social behaviour. An examination of other species of this family that are largely unknown from an ethological point of view would certainly be worthwhile.

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