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Cocoon care in the social spider *Stegodyphus dumicola* (Eresidae)

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Abstract
The evolution of cocoon care in *Stegodyphus dumicola* seems to be influenced by a high migration rate between the colonies. Intruding conspecifics are tolerated by resident spiders and discriminating behaviour is observed only under special conditions. To prevent social parasitism, females care only for their own cocoons and not for those of other females from the same or foreign colonies. I describe biparental cocoon care and two different reproductive strategies that males have developed due to the social organisation in the colonies of *S. dumicola*. This is the first description of biparental care in spiders. Possible causes of biparental care are discussed.

Key words: Social spiders, cocoon recognition, biparental cocoon care, male reproductive strategies

INTRODUCTION

Ecological studies have revealed both the costs and benefits of sociality and have shown that social behaviour is maintained only under special ecological conditions. Spiders are usually solitary, exhibiting aggressive behaviour towards other animals, including conspecifics. Communal and cooperative living patterns have only been observed in a few species from several families.

The genus *Stegodyphus*, which is common in arid regions of Africa, Asia and South America, has three species groups (the *miranda*, *dufouri* and *africanus* groups), each including both social and solitary species, making it a very interesting spider genus for the study of social behaviour (Kraus & Kraus 1988, 1992). The development of permanent social life patterns in *Stegodyphus* seems to be the result of extending the early social stage of brood-caring subsocial species. This could finally lead from communities of juveniles to permanently social colonies. In this context parental care seems to be one of the main steps in the evolution of sociality in *Stegodyphus* (Kraus 1988).

Discrimination of conspecific unrelated individuals is a general phenomenon of true societies and was explained by the concepts of 'inclusive fitness' and 'kin selection' by Hamilton (1964). Several references (Kullmann 1974; Kraus 1988; Seibt & Wickler 1988) to the previous suggestions that spider societies are open systems without kin recognition, contradict the concept of societies in which individuals invest in valuable cooperative efforts. A condition for effective kin selection is that natural selection will favour social or altruistic behaviour if individuals are able to develop in ways that affect their parental care or helping behaviour. No observations of cooperative behaviour should be expected without kin recognition because of the increased risk of social parasitism (Hamilton 1964). But cooperative brood care has been shown several times in permanent

social species of *Stegodyphus* (Kullmann 1974; Kraus 1988).

I will show (1) that colonies of *S. dumicola* are open systems without discriminating behaviour towards conspecifics, and (2) that females of *S. dumicola* care only for their own cocoons.

METHODS

Natural History

Stegodyphus dumicola (Fig. 1) is a common social spider in the thornbush savanna of Southern Africa (Kraus 1988). Colonies consist of 2 to 400 spiders but solitary individuals are often found. Spiders sitting underneath the silky nest show activities like mating, prey capture and guarding of cocoons both during the day and night. Web maintenance activities are performed cooperatively and mainly at night. Feeding takes place below the nest and the spiders mostly share the prey. The first mature males were found in January, the first cocoons were produced in February. The reproductive cycle ends in May/June when all adults are dead, sucked out by the young.

Fig. 1. Female (left) and male (top) of *Stegodyphus dumicola* in the colony.

Observations

Field work was done in 1996 and 1997 in Namibia on the farm Otjiseva in the Khomas Highland 40 km north of Windhoek, and in Khorixas, Damaraland (about 480 km from Otjiseva). The colonies were from different sites and different populations (24 colonies from Otjiseva, 21 colonies from 23 km north from Otjiseva and 40 colonies from Khorixas). Of these, 35 colonies were observed in the natural situation near Khorixas. Some colonies were transported from their place of origin and observed at Otjeseva. During transportation the spiders remained within their nest. Spiders from about 85 colonies were collected and marked individually with fluorescent hair gel (Pop color, Jofrika Kosmetik GmbH) and their length and weight were determined. Cocoons were marked with silk colour (Seidicolor, Germany). The colonies were observed 1996/97 from January to May. They were checked once every hour between sunrise and sunset with respect to: immigration/emigration of males/females, aggressive behaviour, copulations, production of cocoons, cocoon guarding (contact, defensive behaviour, handling), and hatching of spiderlings.

Experiments

Cocoon guarding. To test the benefits of guarding cocoons, field experiments were carried out in Otjiseva. Females in colonies and solitary females (mothers) were removed from their cocoons, which were then inspected during the following 5 to 7 days. As controls, females were removed, marked and returned to their cocoons.

Cocoon care. Cocoon exchange experiments were carried out with 15 colonies and 25 solitary females. Cocoons were removed from the colony, marked and put into a foreign colony. Other cocoons were removed, marked and returned to their original colony. A similar experiment was made with cocoons of solitary females: they were removed and either transferred to the nest of another solitary female, whose own cocoon had been removed, or returned to their original nest (control).

To answer the question whether females care for other females' cocoons in their own

Table 1. Behaviour of *Stegodyphus dumicola* towards intruders in the colony.

Intruding individual	Behaviour of colony members
Juveniles (conspecific)	No aggression: 0% (N = 40)
Females (conspecific)	No aggression: 0% (N = 120)
Males (conspecific)	Sometimes aggression from guarding females and males: 26% (N = 75)
Other spider species	Aggressive attacks: 100% (N = 54)
Foreign animals	Aggressive attacks: 100% (N = 43)

colony, females were removed from the colony and their cocoons were observed for more than a month. The control experiment was to put the removed and individually marked females back into their colony.

RESULTS

Kin recognition

Immigration and emigration of males and females was observed in 94% of the colonies (N = 115). The remaining 6% of the colonies died away due to infection with a fungus. There was no difference in migration behaviour between moved colonies and colonies in their natural habitat. There was no discriminating behaviour from resident spiders towards immigrating conspecific spiders, whether juveniles or adult females (Table 1). Only intruding males were attacked several times by female spiders guarding their cocoons. Immigrated males and females were able to reproduce in the new colony.

Intruding individuals of other spider species (*Nephila senegalensis*, *Stegodyphus bicolor*, *Gandanameno echinatus*) or insects (ants, termites, wasps, bugs) were vigorously attacked by the members of the colony.

Table 2. Hatching success (%) of *Stegodyphus dumicola* cocoons of solitary and colonial females with respect to guarding behaviour

	Solitary		Colonial	
	N	%	N	%
Guarded cocoons	18	12%	15	18%
Unguarded cocoons	20	0%	17	0%

Table 3. Guarding time and hatching success in *Stegodyphus dumicola* in the cocoon exchange experiment.

	Own cocoon N = 27	Exchanged cocoon N = 25	χ^2-test
Solitary females			
Time spent guarding (165 observations)	54%	2%	$P < 0.001$
Hatching spiderlings	11%	4%	$P < 0.05$
Colonial females			
Time spent guarding (276 observations)	17%	0%	$P < 0.001$
Hatching spiderlings	19%	0%	$P < 0.001$

Cocoon guarding

Unguarded cocoons were not able to survive for longer than 3 days. Some cocoons dried out, others were emptied by ants. Spiderlings hatched significantly more often from guarded cocoons than from unguarded cocoons (Table 2; χ^2-test, $P < 0.001$).

Cocoon care

The experiments showed that no exchanged cocoon was guarded in the colonies. Only one solitary female (out of N = 52) guarded an exchanged cocoon and only in this case did spiderlings hatch (Table 3). Cocoons from which the mother had been removed were not guarded by the remaining females in the colony, and no hatching of spiderlings was observed from motherless cocoons. Most cocoons were dried out.

Previously only females have been described as having guarded cocoons. During field observations in 1996 and 1997, however, I found that males were also guarding cocoons. They attacked and killed ants and other intruders that tried to remove the cocoons, even in the absence of the female. In cases (N = 11)

where all females were killed, the males stayed by the cocoons and the spiderlings. This indicates that the males were actually guarding the cocoons, not just guarding the females.

In the situations where males were observed guarding, females and males shared the guarding time (Fig. 2). There was no significant difference between the guarding time of the mother and that of the male. Solitary females and females without a guarding male invested significantly more time in cocoon care than females with a male helping them.

Females whose cocoons were guarded by males were significantly heavier than females without guarding males (females with guarding male: mean ± SD: 157.3 ± 38.0 mg (N = 30); females without guarding male: 116.3 ± 10.3 mg (N = 28); t-test: $P < 0.001$). Many observations showed that the guarding males copulated several times with the mothers on their cocoons (N = 118).

Males of *S. dumicola* seem to follow two different reproductive strategies: guarding and wandering. Guarding males (20% of N = 150) were significantly larger than wandering males (body length 5.6 ± 0.56 mm vs. 5.0 ± 0.61 mm; N = 30 and 120; t-test: $P < 0.001$). They remained in the colony, guarding the cocoons of the larger females and showed aggressive behaviour towards other (intruding) males. Smaller males (80% of all males; N = 150) migrated together in groups of 2-9 to other colonies and copulated with the females there. Afterwards they left the colony and wandered, still as a group, to the next colony. The longest journey observed for a male was about 17 m. I never observed any male-male aggression within wandering groups from the same colony during copulations in foreign colonies. Intruding males first simulated guarding behaviour towards cocoons in foreign colonies (N = 12) and copulated with the mothers on the cocoons. Later they tried to remove these cocoons (N = 9).

Females with a guarding male produce a second cocoon more often than females without a guarding male (13 of N = 30 vs. 1 of N = 28; χ^2-test: $P < 0.001$).

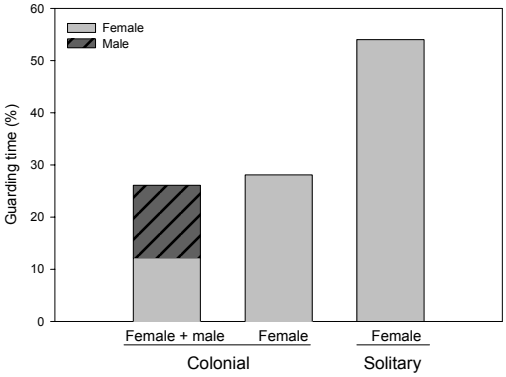

Fig. 2. Cocoon guarding times in *Stegodyphus dumicola*.

DISCUSSION

In many species reproductive success is highly dependent on the quality of parental care (Clutton-Brock 1991). In spiders the adaptive value of cocoon care seems to be the protection of the eggs from predators and parasitoids and the provision of a favourable climate, and also (in some species) helping spiderlings to hatch out of the cocoon. Guarding behaviour in *S. dumicola* is necessary to secure the survival of the eggs, to protect them from desiccation and predators. Previous observations of cooperative parental care in *Stegodyphus* were based mainly on laboratory studies (Kraus 1988, Kullmann 1988). In the field, females of *S. dumicola* cared only for their own cocoons. Cocoon exchange experiments showed that females were able to distinguish between their own cocoons and foreign cocoons from the same or other colonies. This behaviour seems to be adaptive in view of the high migration activity of the spiders and the lack of discrimination towards intruding females. Both factors create a high risk of social parasitism. The ability to distinguish between own cocoon and foreign cocoons was also found in vagrant wolf spiders (Kürpick & Linsenmair in prep.). Observations about cocoon care of social spiders are rare. In species such as *Archaeranea wau* and *Agelena consociata* females care for their own cocoons and all those colonies also show no kin recognition (Buskirk 1981).

Biparental care of cocoons is unusual in spiders. In *S. dumicola* females and males share the guarding time. It is possible that females without a guarding male have less time for foraging and need more energy to ward off predators and parasitoids. Thus females with a guarding male could exploit the advantage to produce a second cocoon. One reproductive benefit for guarding males seems to be the defence of the cocoons against ants and intruding males of *S. dumicola* from foreign colonies. This behaviour is necessary because wandering males showed infanticidal behaviour. Another advantage is, that guarding males also copulated several times with the mothers on their cocoons. Thus, they try to monopolise the fertilisation of the second cocoon.

Smaller males wandered in groups from the same colony to other colonies, copulating with the females there. The intruding males first simulated guarding behaviour, tried to copulate with the females and afterwards removed the female's first cocoon. Infanticidal males were also found in *Stegodyphus lineatus* (Schneider & Lubin 1996). The advantage of wandering in groups of (presumed) relatives to other colonies could be explained by the competition hypothesis: for the smaller males it may be advantageous to find a new colony where they may compete successfully with recident males and avoid competition with large males from their own colony (Moore & Ali 1984). They would increase their inclusive fitness (Hamilton 1964) by inseminating the receptive females in foreign colonies together. Cooperating groups of related males also have better chances to compete with the guarding males in already occupied colonies. Differences in behaviour are of vital importance for variable reproductive advantage and give individuals the chance to choose a promising strategy. In *S. dumicola* alternative strategies according to male size enables optimal reproductive success.

Parental care as in *S. dumicola* is unusual among arachnids and shows an interesting variety of behaviour patterns in the interactions between the sexes to secure reproductive success. It is urgently necessary to start molecular-biological work on paternity and relationship in colonies of *S. dumicola* to confirm or complete the results presented above.

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