

Full Proposal

The evolution of cooperative parental care in spiders

1. The evolution of social systems

Before facing the problem of spider societies, it is necessary to recall some general problems of societies and social behaviour. Ecological studies have revealed both about costs and benefits of sociality and have shown that social behaviour is maintained only under special ecological conditions. Thus sociality need not be necessarily preferred over a solitary lifestyle.

Insights into behavioural traits and ecological conditions that favour sociality could be gained in studies with taxa having both solitary and social representatives.

This chance was used in investigations about socialities of arthropods and two hypothetically paths of social phenomena were defined designated as parasocial and subsocial, characterized by different intermediate levels. Along the first path, eusociality is reached by means of the association of non-related adults that bases further social evolution (Michener 1958). The second case is the result of extension of the early social stage of parental care (Wheeler 1923).

2. Evolution of sociality in spiders

Spiders are usually solitary exhibiting aggressive behaviour toward other animals, including conspecifics. Communal and cooperative living patterns have been observed in a few species from several families (0.2% of about 30 000 species). This is very few in comparison to the evolution of about 12000 (1.2%) social species in insects.

Spider families may have followed both the matrifilial (subsocial) or the aggregational (parasocial) paths of social development. A study of the existing species shows a progression of behaviour levels from solitary to socially complex.

1. Aggregational path → territorial social species (D'Andrea 1987)

Along the aggregational path the intermediate level consists of species that are gregarious in favourable habitats. Their webs are grouped in complexes in which each spider defends a trophic space corresponding more or less to a single hunting web. In a successive group of species aggregation is permanent. The spiders share a common retreat where they do not manifest any type of territorial behaviour, unlike on the webs. These species show no cooperation in parental care.

Examples: *Metepeira*, *Metabus*, *Cyrtophora*

2. Matrifilial path → nonterritorial-social or cooperative species

The matrifilial path is characterized *ab origine*, by the presence of a family web shared by several individuals who manifest a typically social behaviour such as tolerance cooperation in prey capture and parental care (Buskirk 1981; Elgar & Godfray, 1987). The spiders show a high level of relatedness ((Lubin & Crozier 1985; Roeloffs & Riechert 1988; Smith 1994) and a biased sex ratio (Lubin 1991).

Examples: *Anelosimus eximius*; *Stegodyphus*

3. The evolution of sociality in *Stegodyphus*

Following the revision of the genus by O. & M. Kraus (1988) *Stegodyphus*, which is common in arid regions like Africa and Asia has three species groups (*miranda-*

,*dufourii*- and *africanus*-group), each including both various solitary as well as single gregarious species. This strongly suggests three independent evolutionary origins of sociality within the genus *Stegodyphus*, making it the most interesting spider genus with respect to social evolution. The origin of permanently social species in *Stegodyphus* seems to be a transition in the early social stage of the subsocial species caused by brood care from communities of juveniles to colonies of adults (Kraus & Kraus 1988).

In this context parental care seems to be one of the main steps in the origin of sociality in *Stegodyphus*.

The parental care in eresids can be subdivided into two categories

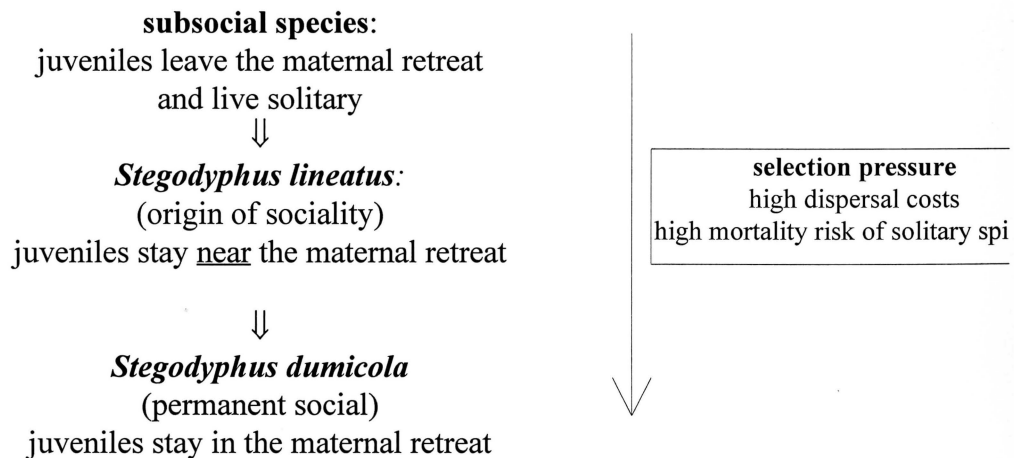
1. Cocoon care

- Attention to cocoons (protection against predators and parasitoids)
- Transport of cocoons (temperature regulation)
- Opening of the cocoon in time for hatching spiderlings

2. Care for the young

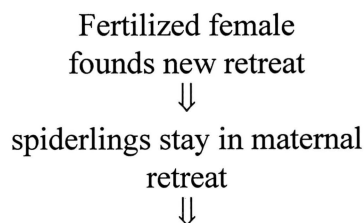
- Feeding the young by regurgitation
- Offering prey to the young
- Gerontophagy (maternal female is sucked out by the young)

Several authors (Wickler & Seibt 1988, Schneider 1991) have tried to describe hypothetically paths to sociality in *Stegodyphus* using the example of the *S. miranda*-group:



This way to sociality may lead to the following suggestion of the foundation of a *S. dumicola*-colony (Wickler & Seibt 1988; Schneider 1991):

Hypothetical foundation of a colony in *S. dumicola*



males fertilize their sisters
 ↓
 high level of inbreeding
 ↓
 theoretically this suggests a high cooperation rate in
 prey catching and brood care (Hamilton 1964)

There are several references in the literature (Kullmann et al. 1974, Seibt & Wickler 1988, Kraus, M. 1988) that permanent social species in *Stegodyphus* show cooperative brood care.

Thus, this provides:

- no distinction between own cocoons and foreign cocoons
- females also care about foreign cocoons
- no discrimination between own young and foreign spiderlings
- females also feed foreign spiderlings

Several hints (Krafft 1982a, Kullmann 1974, Kraus 1988, Seibt & Wickler 1988) that spider societies are open systems stay in contrast to the concept about societies where individuals invest valuable cooperative efforts. Kin selection assumes that natural selection will favour social or altruistic behaviour. If there is no kin recognition found in spider societies no cooperative investigations should be expected because of the increased risk of social parasitism. Discrimination of conspecific unrelated individuals is a general phenomenon of real societies and was explained by the concepts of „inclusive fitness“ and „kin selection“ (Hamilton 1964).

Thus following questions should be examined during the Phd research:

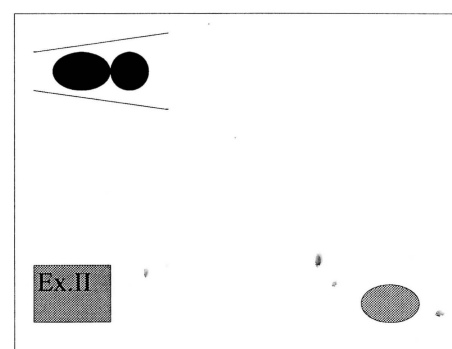
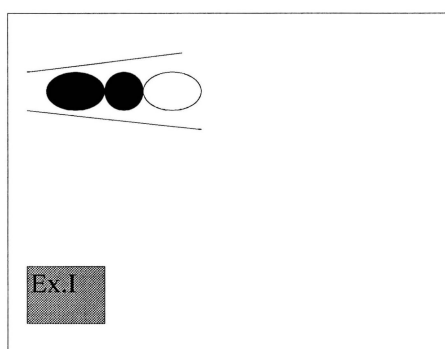
Are there altruistic interactions within the colonie of *S. dumicola*?

Does cooperative cocoon care and cooperative breeding exist in *S. dumicola*?

1995 separation experiments in the laboratory with *S. dumicola* from Namibia were conducted These Experiments showed that:

1: Behaviour of *S. dumicola*-females towards own and conspecific cocoons

Experimental design:



○ own cocoon
from the

● foreign cocoon
same colony

control:

Own cocoon was removed and then offered to the female again.

(n=15)

Result:

Females accepted their own cocoons, sitting on the cocoon in 94%

treatment:

Foreign cocoon from the same colony offered to the female

(n=17)

Females did not accept foreign

100%

2. Separation experiments with 2 females of *S. dumicola*

2 separated females from the colonies were observed

1. Two females without cocoons
2. One female with cocoon and one female without a cocoon
3. Two females that had produced a cocoon

Result:

| experiment | retreats | aggressions | n |
|---|----------|--|------|
| two females without cocoons | 1 | no aggressions | n=13 |
| one female with cocoon one female without a cocoon | 2 | in 7 cases aggressions were observed several times | n=9 |
| two females with cocoons | 2 | no aggressions | n=7 |

3. Change experiments with cocoons between undisturbed colonies

I. Cocoons were removed from the colony and later taken again into the web of the own colony.

The females invested further attention to the cocoons

II. Cocoons were removed from the colony and taken into the web of a foreign colony

The females ignored the foreign cocoons.

These laboratory experiments showed, that females take investigate only their own cocoons and it seems possible that cocoon recognition is found in *S. dumicola*.

Thus following questions and experiments should be examined during the research in Namibia:

1. Are there altruistic interactions within the colony?

Are there asymmetries in the performance of individuals concerning cooperative activities for the colony.

Method:

- The individuals of several colonies will be marked and their length and weight will be determined.
- The spiders (reproductive and non-reproductive) will be observed whether and how long they invest work (like building and cleaning the web; prey catching)
- Could we find females that invest parental care in the brood of other females

2. Does cooperative cocoon and cooperative brood care exist in *S. dumicola*?

1. Cocoon care:

Does cooperative cocoon care exist in *S. dumicola*?

Laboratory experiments showed that the females did not cooperate in cocoon care. This result was unexpected and possibly due to laboratory artefacts. A reexamination of cocoon care under natural conditions is therefore urgently necessary.

Observations should be carried out with respect to risks of parasitism and predatory pressure for cocoons under natural conditions. The results of these experiments would give insights into cocoon care in *S. dumicola*.

Method:

- The individuals of several colonies will be marked and their length and weight will be determined
- observations with respect to following aspects will be carried out:
 - which females take care of cocoons
 - Do females change their behaviour towards reversed cocoons
 - Separated females will be removed from their cocoons. The cocoons will be controlled regularly in comparison to guarded cocoons in respect to parasitism and predatory pressure

2. Recognition of the young

There was no possibility to carry out investigations with respect to the recognition of the young in the laboratory, because the cocoons mostly contained non-fertilized eggs. Thus, it is necessary to carry out observations in the field to get answers and that helps also to enable effective raising of *S. dumicola*.

Method:

- The individuals of several colonies will be marked and their length and weight determined
- observations with respect to the following aspects will be carried out:
 - which females feed the young (own young or the spiderlings of other females)
 - change experiments with spiderlings;
 - change experiments with heavier and lighter; younger and older juveniles

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