

## Sibling Recognition and Nepotism in the Subsocial Funnel Web Spider, *Cælotes terrestris* (Araneae, Amaurobiidae)

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**ABSTRACT:** Cooperative or non-territorial permanently social spiders are believed to have evolved from species showing subsocial maternal care. The transition from subsocial to cooperative social groups probably involved a transition from an outbreeding breeding system to one with inbreeding. Nepotistic recognition among siblings should facilitate the evolution of social cooperation through avoidance of inbreeding and maintenance of mutual tolerance between siblings. We conducted experiments to determine whether a mechanism for sibling recognition is present in the subsocial spider, *Cælotes terrestris* which displays extended maternal care in the form of food provisioning. The numbers of surviving individuals within unfed groups were observed and compared between non-sibling groups of ten spiderlings and groups of ten siblings. The number of survivors differed significantly between groups, with consistently fewer spiderlings surviving in the non-sibling groups than the sibling groups over the study period. This result suggests that sibling recognition and nepotism do occur in this subsocial species. The nepotism involved in the maternal social organization of the *Cælotes* might be an example of a preadaptation facilitating the evolution of permanent social life.

**Key words:** *Cælotes terrestris*, Nepotism, Sibling recognition, Subsocial spider

### INTRODUCTION

Spiders are generally solitary animals. Most species do not even distinguish members of their own species from other prey, so that one may devour another when opportunity arises (Kaston 1965). There are, however, 23 species of social (cooperative or non-territorial permanently social) spiders in seven different families (D'Adréa 1987, Avilés 1997). In social spiders, group members live together throughout their lives in a communal nest. Spiders within a social group cooperate in prey capture, nest construction, and possibly brood rearing (Kullmann 1972, Kraft 1979, Buskirk 1981). Researchers believe that these species evolved from species showing subsocial maternal care (Kullmann 1972, Horel and Krafft 1986, Kim and Horel 1998).

The transition from subsocial to cooperative social groups would have involved a transition from an outbreeding system to one with inbreeding (Whitehouse and Lubin 2005). Individuals that avoid mating with close relatives or optimally outbreed may accrue fitness benefits over conspecifics that mate randomly (Waldman 1988, Lehmann and Perrin 2003). Kin recognition or kin discrimination can also facilitate the evolution of social cooperation through inclusive fitness benefits accrued by individuals cooperating with close relatives (Hamilton 1964).

The benefits of kin recognition or kin discrimination systems

include providing opportunities for nepotism (favorable treatment of kin; Hamilton 1964). Nepotistic recognition between siblings should be important in spiders which display extended group living, such as maternal social species. However, while subsocial spiders may also stand to benefit from nepotism, sibling recognition has not been studied in any subsocial spider (Whitehouse and Lubin 2005).

Spiderlings of *Cælotes terrestris* (Araneae, Amaurobiidae) live in a group inside the natal nest with their mother for about one month after emergence from the cocoon before they disperse to pursue a solitary life (Gundermann 1989). Greater prey availability on the maternal web prolongs the gregarious period for spiderlings of this species (Krafft et al. 1986). Maternal provisioning is one of the most important factors that prevent sibling cannibalism (Gundermann et al. 1988), and maternal presence, even when there is no prey on the web, leads the spiderlings to stay in a highly tolerant group during the period of maternal care. Siblings reared with their mother survived better than siblings reared without their mother in the no-food condition (Gundermann et al. 1993). Does the mechanism maintaining mutual tolerance among siblings in this species involve only maternal influences and food conditions?

The objective of this study was to determine whether tolerance among siblings of the subsocial funnel web spider, *C. terrestris* involves nepotistic kin recognition. Tolerance within sibling groups of this species was compared to that of non-sibling groups in the absence of food or adult females, to exclude influences of food

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availability and maternal presence.

## MATERIALS AND METHODS

### Study Species

*Cælotes terrestris* Wider (Araneae, Amaurobiidae) is fairly common throughout European woodlands (Tretzel 1961). The female spider weaves a silken tube in shaded places such as under stones in forest litter, in the bark of dead logs, etc. The female then constructs an egg sac inside this retreat area. From a lenticular egg sac, 40 to 60 spiderlings emerge, stay in a group inside the tube with their mother for about one month, and then disperse to lead a solitary life (Gundermann 1989).

### Collection and Laboratory Rearing

Female spiders were collected during May in a forest in Nancy, France (Northeast France, elevation: 217 meters, latitude: 48° 41'N, longitude: 06° 13'E, annual temperature:  $9.6 \pm 6.3^\circ\text{C}$ , annual precipitation: 74 cm). By May, most females have already been inseminated in the field (between early April and late May 80% of the females collected in the same area laid viable eggs in the laboratory; Gundermann 1989).

Our experiments were conducted under laboratory conditions, as natural nests are located in inaccessible spaces. The female spiders (potential mothers) were transferred to a room maintained at  $20 \pm 2^\circ\text{C}$  and lit by fluorescent lights (approx. 100 lx, 12L/12D light cycle), and introduced into glass terraria (one female per terrarium; L: 200 × W: 120 × H: 200 mm) of a type originally designed by Gundermann et al. (1993) to study mother-offspring interactions and dispersal behavior of *C. terrestris*. Each terrarium was filled on one side with a block of plaster and on the other with a mixture of sand and peat 70 mm deep. On its outer side the plaster block had a gallery in the form of a tube (diameter: approx. 12 mm) with openings on the upper and both side surfaces of the block. These openings facilitated removal of spiderlings from the maternal retreat. Throughout the experiment the terraria were humidified twice a week and liberally provided with 20 ( $\pm 2$ ) mg cricket larvae.

Terraria were examined twice a day. Following introduction into the terrarium, the females rapidly settled into the gallery, and within a week each had woven a tube prolonged by a small funnel-web from the gallery out the open space. A couple of weeks later they oviposited and started guarding their egg sacs.

### Experimental Design

Two types of experimental groups were formed: 1) sibling groups of 10 individuals from a single clutch ( $N=21$ ), and 2) non-sibling groups of 10 individuals, each from a different clutch ( $N=21$ ). The

groups of ten spiderlings were transferred from the terraria to transparent plastic boxes (L:75 × W:160 × H:90 mm, with a grilled window in the lid for aeration) for observations at close range. To promote web construction, one corner of the box was darkened by covering it with black paper. We also covered this corner with a transparent film to prevent the spiders from spinning against the lid of the box. A piece of cotton placed in a corner of the box was regularly humidified.

Spiderlings used for the experiment were all the same age (the first instar after emergence from the cocoon). For the non-sibling group, spiderlings were selected from clutches that emerged on the same day so that the individuals were in the same developmental period. 21 clutches were used to form sibling groups ( $N=21$  groups) and 21 additional clutches of the same age were used to form non-sibling groups of 10 individuals where each individual came from different clutch ( $N=21$  groups).

The spiderlings were not fed during the experiment, but were provided with water. Each group was inspected daily. We recorded the number of survivors in each group on the 2<sup>nd</sup>, 5<sup>th</sup>, 8<sup>th</sup>, 11<sup>th</sup>, 14<sup>th</sup>, 17<sup>th</sup>, 20<sup>th</sup> and 23<sup>rd</sup> day after group formation. (*Cælotes* spiderlings are usually inactive. Therefore, direct observation of nepotistic or agonistic acts between individuals is problematic, especially over short time-periods.)

The body mass and body length of each spiderling was measured on the transfer day, and mean body masses did not differ between the experimental groups. The mean body masses of spiders in sibling groups and non-sibling groups were  $1.37 \pm 0.67$  mg (mean  $\pm$  SD) and  $1.40 \pm 0.55$  mg respectively (Mann-Whitney U test:  $U = 201.5$ ,  $n_1 = n_2 = 21$ ,  $p = 0.6327$ ), and the mean body lengths of spiders in the sibling and non-sibling groups were  $5.14 \pm 0.99$  mm and  $5.35 \pm 0.87$  mm respectively (Mann-Whitney U test:  $U = 175.5$ ,  $n_1 = n_2 = 21$ ,  $p = 0.2576$ ).

### Statistical Analysis

The Friedman test was used to examine reductions in the number of survivors within each group type over the observation period, and repeated measures ANOVA was used for comparison of the number of survivors throughout the observation period between the groups. I conducted regression analysis to determine the rate of change (regression coefficient) in the number of survivors from the 2<sup>nd</sup> day after installation for each group type, and used the two-tailed Student's *t* test to test the hypothesis that the two group regression coefficients were equal.

## RESULTS

The number of spiderlings alive within the group decreased sig-

nificantly over the observation period in both experimental groups (Friedman test, sibling group:  $\chi^2 = 94.7$ ,  $df = 8$ ,  $p < 0.0001$ ; non-sibling group:  $\chi^2 = 136.5$ ,  $df = 8$ ,  $p < 0.0001$ ). However, the number of survivors differed significantly between the groups, with fewer spiderlings surviving in the non-sibling group than the sibling group in each time interval (Fig. 1; Repeated measures Anova:  $F_{[8,320]} = 2.942$ ,  $p = 0.0035$ ). This result suggests that sibling recognition involving nepotism occurs in this species.

Mortality in the non-sibling group was highest between group formation and the second day after group formation ( $11.4 \pm 13.2\%$ ), while no mortality was recorded in the sibling group during this period. Regression analysis of the rate of change in the number of survivors in the two groups (removing the effect of decreased survivorship on the second day) did not detect a significant difference between the sibling group and non-sibling group (Fig. 2; Regression equation:  $y = -0.158x + 10.351$  ( $R^2 = 0.268$ ) for the sibling group and  $y = -0.195x + 9.429$  ( $R^2 = 0.349$ ) for the non-sibling group; two tailed Student's  $t$  test for equality of the regression coefficients for the two groups:  $t = 0.4123$ ,  $df = 12$ ,  $p > 0.5$ ). This result suggests that first encounters play a critical role in sibling and non-sibling recognition.

## DISCUSSION

The results of this study suggest that kin recognition and nepotism are involved in mutual tolerance between siblings of *Caelotes terrestris* during the initial days of the maternal social period. Mortality within the sibling groups was lower than that in the non-sibling groups when the spiderlings were not provisioned.

During the maternal period, *C. terrestris* agonistic behavior toward siblings has been observed, but this behavior is generally

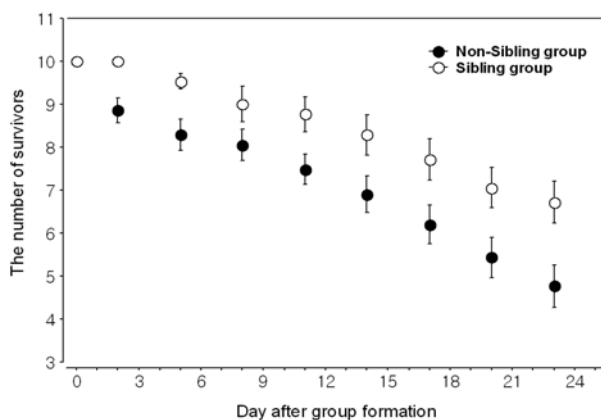


Fig. 1. Comparison of the number of survivors over the 24-day period after group formation in sibling groups and non-sibling groups of spiderlings (mean  $\pm$  SD).

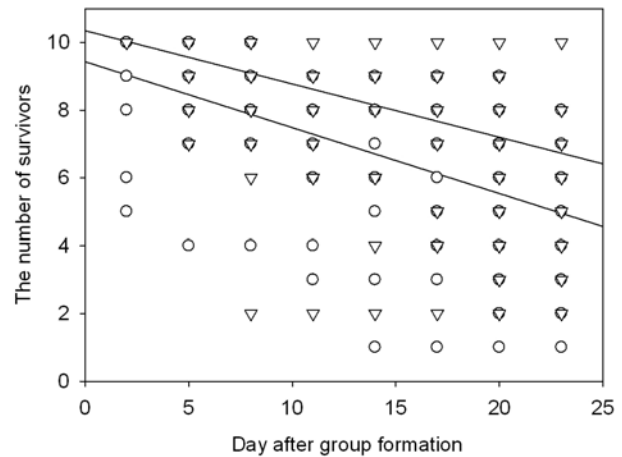


Fig. 2. Comparison of the regression slopes of Sibling group ( $\nabla$ ) and Non-Sibling group ( $\circ$ ) after removed the mortality effect of second day. Upper regression line represents Sibling group and lower line represents Non-Sibling group. The slopes of the groups were not significantly different.

non-lethal, and individuals stay in groups (Gundermann 1989). *C. terrestris* mothers capture prey struggling in the web and transfer the food to their offspring, which reduces the risk of sibling cannibalism within the clutch (Gundermann et al. 1992). However, motherless or food-deprived spiderlings exhibit threat displays, fights, and cannibalistic acts at higher rates than normally-fed spiderlings or those kept with the mother (Gundermann et al. 1993). It appears evident that maternal care and prey availability are important factors maintaining mutual tolerance among siblings and preventing sibling cannibalism. The results of this study suggest that sibling recognition and nepotism are also important factors affecting mutual tolerance and rates of cannibalism in groups of *C. terrestris*.

Spiderlings were observed feeding on the dead bodies of group-mates in both experimental conditions. However, it is not certain whether the cannibalized spiderlings died as a result of intra-group aggression or by starvation or other causes. Aggression and mutual avoidance were observed in both types of groups, but our observations suggest that individuals in the non-sibling group maintained larger inter-individual distances, while siblings were much more cohesive, suggesting avoidance of close proximity in non-sibling groups. Further quantitative studies are needed to examine behavioral differences between group types in detail.

*Diaea ergandros*, a social crab spider, accepts immigrant spiders into their kin-based groups (Evans 1999). Evans (1999) observed that juvenile *D. ergandros* preferentially ate unrelated spiders rather than siblings, and that subadult females cannibalized unrelated immigrant females and related males instead of immigrant males when starved. These observations suggest that immigrants might represent

a food reserve in times of food shortage, and that subadult female spiders may maximize outbreeding opportunities by sparing unrelated males (Evans 1999). *Celotes terrestris* disperse from the natal nest by means of walking, not by ballooning, so their dispersal distances are relatively short (Gundermann 1989). In the field it is possible that adult spiders routinely encounter their siblings, which means that sibling recognition might help spiders to avoid cannibalizing their siblings and promote inbreeding avoidance.

Maternal grouping is the probable origin of the subsocial route leading to permanent social organization (Wilson 1971, Kullmann 1972, Buskirk 1981, Plateaux-Quénu et al. 1997). The nepotism involved in the maternal social organization of the *Celotes* may be considered as a preadaptation for evolution of permanent social life.

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