Maternal Influence on Spiderlings' Emergence from the Cocoon: Observations in a Subsocial Spider

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ABSTRACT: Brood caring behavior was observed in *Amaurobius ferox* (Araneae, Amaurobiidae), a semelparous subsocial spider, from cocoon construction until the emergence of spiderlings from the cocoon. Unlike most spiders, which emerge from cocoon by their own means, *A. ferox* mothers intervene in the process of the emergence of their young. I manipulated broods by removing the mother prior to emergence to determine the effects of maternal behavior on the emergence of spiderlings. My results showed that maternal intervention making the cocoon expansion and its exit, is not absolutely necessary for the emergence of *A. ferox* spiderlings from the cocoon. Nine clutches out of ten were able to get out of the cocoon by their own means without their mother's help. There was no difference between control groups ('with mother') and experimental groups ('without mother') in the number of spiderlings that emerged (96.9 ± 25.3 vs. 90.4 ± 14.2, respectfully) and in the time from the beginning to the end of emergence (36 ± 12 vs. 41 ± 17 hours). Time from eclosion until the emergence of the first individual in a clutch, however, was greater in the mother-absent group (3.5 days) than in the control group (2.0 days). The construction of the cocoon by the mother required always occurred in the same area within the retreat, and took approximately 6 hours, and the mother guarded the eggs during the incubation period. The emergence of the spiderlings followed a sigmoidal pattern. After emergence, the spiderlings formed a very compact group on the cocoon, which may be important in securing maternal care. The absence of cribellum and calamistrum, structures likely involved in their survival, observed in individuals of the first instar suggests that in the first stage of life, the spiderlings are dependent on their mother.

Key words: *Amaurobius,* Brood emergence, Maternal care, Spiderlings, Subsocial

INTRODUCTION

Contrary to the popular image of spiders as solitary, some species live in populous societies (possibly exceeding 10,000 individuals), building impressive silky structures (see Avilès 1997, Vakanas and Krafft 2001, Salomon and Lubin 2007). Complex social organization, however, is rare in spiders. Among approximately 30,000 species of spiders, there are only around 30 non-territorial permanently social species (Krafft 1979, Buskirk 1981, D'Andréa 1987, Avilès 1997). On the other hand, a number of spider species display a form of social organization that is neither solitary nor truly social (see Kullmann 1972, Buskirk 1981, D'Andréa 1987). Such an organization is considered to be an intermediate form between having a complex social organization and being solitary, and might provide interesting information about the evolution of sociality in animals (Kullmann 1972, Krafft 1979). *Amaurobius ferox* (Araneae, Amaurobiidae) is an example of such a subsocial spider.

A female *A. ferox* constructs only a single egg sac in her lifetime (Lemasle 1977). In this semelparous species, mothers show extended and systematic brood caring behaviors (see Kim and Horel 1998, Kim and Roland 2000). Mother provides her young with a batch of trophic eggs 1~2 days after their emergence, which the young immediately devour (Kim and Roland 2000). The young then molt 3~4 days later (Kim 2001) and matriphagy occurs 1~2 days after this first post-emergence molt (Kim and Horel 1998). Mothers are always devoured by their young (Kim et al. 2000). After their mother's death, the brood assumes a temporary form of social organization (Kullmann 1972, Kim et al. 2005ab), as the siblings remain in their natal nest for 3~4 weeks until dispersal (Kim 2000).

Tahiri et al. (1989) observed a remarkable behavior in *A. ferox*. On the 15th or 16th day of the incubation period, the female produces a skein of silk thread, one extremity of which is fixed to the egg sac and the other extremity is tugged and then fixed to a wall surface of the retreat in the web. After the silk threads are fixed, a spontaneous contraction of the threads causes distension of the cocoon. Tahiri et al. (1989) noticed that the emergence of *Amaurobius* spiderlings from the cocoon occurred 2~3 days later. Millot and Bourgin (1942) also recorded distension of the cocoon before emergence in the subsocial spider, *Stegodyphus lineatus* (Eresidae),

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but the behavior of the females of that species have not been examined closely. On the other hand, Bonnet (1946) observed that mothers of the subsocial spider *Dolomedes plantarius* (Pisauridae) gradually distended the egg sac during the spiderlings' development inside the egg sac, while moistening it. Fujii (1978) also suggested, in the subsocial spider *Pardosa astrigera* (Lycosidae), that distension of the cocoon created space for the spiderlings to perform one or more molts inside the egg sac. *A. ferox*, however, does not molt inside the egg sac. Previous studies have not yet determined whether the distention of the egg sac facilitates the hatching of the spiderlings.

In most spider species, spiderlings emerge from the cocoon by their own means. This is universal in cases where mothers abandon their cocoons after construction, but it is also true in the subsocial spider, *Cœlotes terrestris* (Agelenidae) where the mother provides brood care over a prolonged period (Gundermann 1989). Indeed, opening of the egg sac by mothers has been reported in a number of spiders: in Lycosidae (Engelhardt 1964, Eason 1964, Eason and Whitcomb 1965, Rovner et al. 1973, Vannini et al. 1982, 1986, Whitcomb et al. 1966), in certain species of Oxyopidae (Randall 1977), and in Eresidae (Jacson and Joseph 1973). Experimental studies in these species showed either that maternal intervention was necessary for the offspring to be able to exit from egg sac, or that it had no visible effect, depending on the species.

Although Tahiri et al. (1989) described maternal intervention in the emergence process of *A. ferox* spiderlings, they did not examine the function of this maternal behavior. I conducted this study of the effects of maternal behavior by comparing the characteristics of emergence in the presence or absence of the mother. I also observed the spiderlings' behavior in the course of the emergence process, and counted the number of individuals emerging from the egg sac, as well as recording some structural features of the young that may have been functionally related with the value of maternal care for the young in the very early stages of life in this animal.

MATERIALS AND METHODS

Study Animal

Amaurobius ferox Walckenaer (Araneae, Amaurobiidae) is commonly found in Europe (Cloudsley-Thompson 1955, Bristowe 1958) with total female body length of 8.5∼14 mm, and body mass of 140∼320 mg (Lemasle 1977). The females spin their cribellate webs under stones in the forest litter, in holes in old walls, and in other secluded places (Cloudsley-Thompson 1955, Tahiri et al. 1989) to capture prey and to provide a protective retreat (Tietjen 1986, Opell 1994). A female constructs a single egg sac in the early summer.

Collection and Rearing

This study was carried out under laboratory conditions to facilitate manipulation of clutches and because the usual locations of naturally-occurring *A. ferox* webs precludes any detailed observation in the field. Inseminated females were collected in June and July, i.e., before the egg-laying period, from under fallen stones and in ruined walls in the forested area of Nancy, France (Northeast France, 48° 41' N, 6° 13' E, elevation: 217 m, annual temperature: $9.6 \pm 6.3 \,℃$, annual precipitation: 74 cm). Insemination was verified by the presence of a mating plug (Suhm et al. 1996).

The animals were housed individually in a glass terrarium ($20 \times 12 \times 20$ cm) containing a block of plaster on one side and a mixture of sand and charcoal (70 mm deep) on the other (Gundermann et al. 1993), and the terraria were humidified twice a week. The spiders were fed 20 (± 2) mg of cricket (*Gryllus dimaculatus*) larvae and were maintained at a temperature of $20\,℃$ ($\pm 2°$) with a 12/12 hour light-dark cycle. Fluorescent lights supplied approximately 100 lux.

Observation and Measurement

I observed egg sac construction and egg-laying behavior by 16 females by direct observation and using stereomicroscopy (Zeiss). I then observed female behaviors toward the cocoon, and recorded the number of spiderlings coming out of the cocoon every 2 hours from the time of eclosion (The cocoon assumes a soft grey color at eclosion.).

Group cohesion is an important characteristic affecting mother-offspring interactions as well as social relationships among spiderlings (Kullmann 1972). The spiderlings should stay close together in a group after emergence to facilitate maternal food provisioning (see Kim and Roland 2000). However maternal behavior at the time of emergence might affect the spiderlings' grouping behavior. Thus, I also observed the grouping behavior of the spiderlings during the process of emergence.

In order to study the spiderlings' grouping behavior, it was necessary to devise a quantification method that met several conditions while being reasonably precise. Specifically, the method had to be consistent enough to allow repeated measurements over a period of time, and it must not disturb the spiderlings. Thus, I evaluated grouping behavior by determining the maximal volume (in the form of parallelepiped rectangle) that the clutch occupied. I measured the spatial distribution of the spiderlings in the maternal web in the terrarium every 8 hours after the beginning of emergence ($n = 14$ clutches).

I also observed structural features, i.e., the cribellum, calamistrum and chelicerae, which are morphological characteristics that may affect the survival of the spiderlings, in newly hatched spi-

derlings. (Cribellum and calamistrum are the organs producing cribellate silk structure. And chericerae are used not only for subduing prey and for defense, but also serve as pliers for all kinds of grasping; therefore they have been referred to as the spider's hands [Fœlix 1996].) Observations of individual web-weaving behavior were conducted on 15 spiderlings placed individually in small tubes.

Experimental Manipulation of Maternal Influence

In order to study maternal influence on emergence of the spiderlings, I performed two treatments. For control groups, the clutch was left with mother through the end of emergence ($n = 10$ clutches), while in experimental groups, the mother was removed from the clutch after eclosion ($n = 10$). I recorded the time elapsed between eclosion and emergence in each clutch, and counted the number of spiderlings emerging from the cocoon. I then observed the grouping behavior of the spiderlings at the end of emergence.

Statistical Analysis

Statistical Analyses were performed with version 5.0 of StatView (SAS Institute, 1998). I used Spearman rank correlation, a non-parametric measure of correlation, to describe the relationship between the number of spiderlings emerging in a clutch and the duration of emergence. The spatial distribution on the web of the spiderlings was compared by repeated-measures ANOVA with different times in the emergence process as a repeated measure. The volume of the group measured at two different times was compared using Wilcoxon signed-rank test. The time delay between eclosion and emergence was compared in the control (with the mother) and experimental (without the mother) groups using Mann-Whitney U test. The duration of emergence and the number of spiderlings emerging from the cocoon were also compared between groups using Mann-Whitney U test.

RESULTS

Cocoon Construction

Cocoon construction required approximately 6 hours. The behavior of the female was comprised of three sequences. 1) Weaving the cupule: First, the female wove the cupule, the lower part of the egg sac in which the female lays its eggs, with ecribellate silk. The weaving process lasted an average of 3 hours. 2) Egg laying: Next the female emitted the eggs, which took $20 \sim 30$ minutes. The female held its opisthosoma in contact with the cupule for several minutes, and then it performed a series of slow contractions, which increased in amplitude over time, and began emitting eggs. Initially, eggs were mixed with a yellowish or light pink liquid, which hardened

in several seconds and disappeared as the eggs became more individual. The female remained on the eggs while contacting its opisthosoma for several minutes. 3) Closure of the cocoon: Finally, the female surrounded the eggs with a thick cribellate silk layer, which took approximately two and a half hours. The cocoon was light pink and lenticular in shape with an $8 \sim 12$ mm diameter, and the lower surface was more convex than the upper surface.

The cocoons of *A. ferox* were always placed in a similar localization within the retreat, both in the laboratory and in the field. It was situated at the top of the retreat, on the ceiling or side of the retreat tube, never in the lower area.

Egg Guarding

During the 19-to-20-day incubation period, the female remained on or near to the cocoon most of the time. However, I have observed cocoons being destroyed by the mother, in which case the silk envelope of the egg sac was consumed along with the eggs. Most of destroyed cocoons appeared manifestly abnormal: with visible blackening, drying or absence of development. However, egg eating by the mother did not appear to always involve abnormal cocoons. Females have also been observed consumed eggs of normal appearance. However, the frequency of such maternal oophagy was not very high (about 5%), and I have never observed a mother devouring its offspring after emergence.

Egg Sac Opening and the Emergence of Spiderlings

Eclosion occurred $17 \sim 18$ days after the construction of the cocoon. Eclosion was associated with a change in the appearance of the cocoon, which expanded and became grayish. Thus the date was easily recorded, even though the silk layer of the egg sac made it impossible to directly observe the individuals inside.

The mother began biting and tearing the surface of the egg sac $1 \sim 2$ days after eclosion. She repeatedly ($6 \sim 15$ times) bit the egg sac in the same place at an increasing rate, which made a hole out of which the spiderlings slowly emerged. The mother continued to bite the egg sac until about twenty spiderlings emerged, which took $15 \sim 20$ hours.

The whole process of emergence of the spiderlings (92 ± 20 individuals per clutch, $n = 16$) took 34 ± 7 hours on average. Fig. 1 shows the timing of emergence for individuals within the clutch, which followed a sigmoidal curve. There was not a significant relationship between the number of spiderlings emerging in a clutch and the duration of the emergence process (Spearman correlation test: $r = 0.167$, $p = 0.532$).

Grouping of the Spiderlings

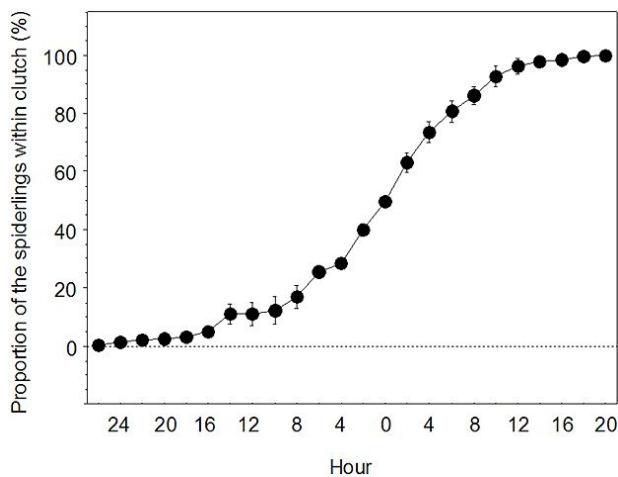The spatial distribution of the spiderlings varied over the course

Fig. 1. The proportion (%; mean ± SE) of spiderlings in a clutch that were found outside of the cocoon at each time interval during the process of emergence ($n = 15$ clutches). The zero hour corresponds to the time at which 50% of the individuals in each clutch had emerged.

of emergence (Repeated measures ANOVA using measurements at 8-hour intervals: $df = 13$, $F_{[3,39]} = 7.351$, $p = 0.0005$). Fig. 2 presents the mean area occupied by spiderling groups at each time interval, which reflects variation in the distribution of the spiderlings on the web during emergence. The spiderlings dispersed over the web immediately after emerging from the cocoon. The spiderlings remained dispersed until approximately the 16th hour, when the average volume occupied by the young was 4.4 ± 2.4 cm^3 ($n = 14$). This wide dispersion among individuals was probably due to disturbance resulting from the behavior of the mother while it was
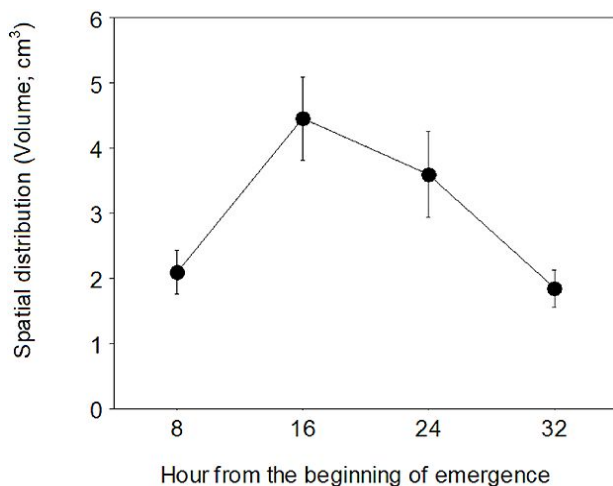

Fig. 2. The spatial distribution of the spiderlings (volume; mean ± SE) over the course of emergence ($n = 14$ clutches). The X-axis corresponds to the time from the beginning of emergence.

opening the cocoon. As soon as the mother ceased tearing the egg sac, the spiderlings stopped moving away, and the spiderlings formed a compact group near the cocoon at the end of the emergence. At the end of emergence, the volume of the group was 1.8 ± 1.1 cm^3 on average (Wilcoxon test; comparison between the 16th and 32nd hours: $n = 14$, $z = 2.7$, $p = 0.0063$).

Cribellum and Calamistrum

In first-instar spiderlings, the cribellum and the calamistrum had not yet fully developed ($n = 15$ clutches). I did observed no traces of calamistrum on the metatarsus of the fourth pair of legs. Only in the second instar (after the first molt), did I observe 9 to 12 hairs on the line constituting the calamistrum, and the cribellum appeared as a thin trait on the spinnerets. Observation of spiderlings isolated in small tubes ($n = 15$) confirmed that individuals of the first instar produced only cribellate silk, whereas both silk types (cribellate and ecribellate) were produced by individuals of the second instar.

Chelicerae

Chelicerae of the first instar spiderlings were transparent and flexible, and did not appear to be functional ($n = 15$). Chitinization on the chelicerae appeared after the first molt.

Functional Value of Maternal Intervention

Emergence of the spiderlings was observed in all clutches in the control group, where the mother stayed with the cocoon ($n = 10$). In the experimental group, where the mother was removed from the cocoon after eclosion, one of the ten clutches did not emerge from the cocoon. Later examination of the non-emerging clutch showed that the individuals had succeeded in eclosion, but had subsequently died inside the cocoon.

In all clutches of the control group, the first spiderlings exited from the cocoon on the second day after eclosion. On the other hand, in the experimental group, the emergence began significantly later, on average three days after eclosion (Table 1).

The number of individuals emerging from the cocoon showed no difference between the groups (see Table 1). An examination of the egg sac after emergence confirmed that almost all spiderlings came out in clutches of both groups. The duration of emergence was also not different for the two groups (see Table 1).

In the experimental group, from which the mother was absent, the spiderlings also gathered near the cocoon in the course of emergence ($n = 9$ clutches). The individuals did not disperse over the web at any time during emergence. However, if I gently and repeatedly touched the web, this disturbance provoked dispersal of the spiderlings on the web. However the spiderlings aggregated into a compact group by the cocoon again within 6~10 hours.

Table 1. Maternal influence on the emergence of the spiderlings from the cocoon   (mean ± SD)

	Successful clutches	Interval between eclosion and emergence (days)	Number of spiderlings emerging	Duration of emergence (hours)	Behavior after emergence
With mother (*n* = 10)	10	2.0 ± 0	96.9 ± 25.3	36 ± 12	Grouped
Without Mother (*n* = 10)	9	3.5 ± 1.1	90.4 ± 14.2	41 ± 17	Grouped
Mann-Whitney U Test		*U* = 10.0, *p* = 0.0043	*U* = 36.5, *p* = 0.4877	*U* = 49.5, *p* = 0.4270	

DISCUSSION

My results showed that maternal intervention was not essential for the emergence of spiderlings from the cocoon in *Amaurobius ferox* in most cases. Nine out of ten clutches come out of the cocoon by their own means, and there was no apparent difference in the duration of emergence compared with those of clutches helped by the mother. However, the time interval from eclosion until emergence of the first individual was substantially longer in the mother-deprived group. In *Peucetia viridans* (Oxyopidae), as well, the young succeeded in coming out of the cocoon without maternal help (Randall 1977), and the delay between eclosion and emergence in the mother-deprived group observed in this study of *A. ferox* was also observed in *P. viridans*, with a delay of 3～4 days. However, this delay led to cannibalism among *P. viridans* spiderlings inside the egg sac (Randall 1977), whereas in *A. ferox* there was no difference between the experimental group and the control group in the number of spiderlings that emerged.

The cocoons of *A. ferox* were consistently placed in a specific localization in the top of the retreat, never in the lower area. This placement may prevent the development of mold on the cocoon, by keeping it out of direct contact with water. Site choice has been shown to have an important effect on cocoon survival in studies of *Nephila clavipes* (Christenson and Wenzl 1980) and *Misumena vatia* (Morse 2007).

During incubation, the female remained near the cocoon most of the time. The function of this maternal behavior was not examined in this study. However, studies of a sympatric subsocial spider, *Coelotes terrestris*, showed antipredatory and antiparasitic effects of maternal presence near the cocoon (Horel and Gundermann 1992, Gundermann et al. 1997). Egg guarding behavior in *Amaurobius* may have the same function, although the antipredatory role is probably less crucial in *A. ferox*, because of the defensive properties of cribellate silk (Tietjen 1986, Opell 1994). Few studies have been conducted on predators and parasites of *Amaurobius*. However, I have observed that insects and ecribellate spiders had difficulty entering the web of *Amaurobius* because of the adhesive property of cribellate silk (Opell 1994), whereas cribellate spiders (e.g., *Amaurobius fenestralis*) entered the web easily. Resident *Amaurobius* spider displayed agonistic behaviors when an intruder appeared, and the intruder generally ran away (personal observation). However, I have also observed fights between resident *A. ferox* and intruders, which sometimes resulted in the death of one of the combatants. *Amaurobius* spiders may be susceptible to parasites, as I have observed dead *Amaurobius* individuals with the opisthosoma covered with fungus (12 observations in the nature, 16 in the laboratory). In addition, acarids were regularly found in *Amaurobius* webs.

I observed that *Amaurobius* mothers consumed their cocoons in this study, although the behavior was not commonly observed in this species. Maternal oophagy has also been reported in other spider species: Clubionidae (Shaw 1989), Pholcidae (Downes 1987), Diplurridae, Desidae and Linyphiidae (Willey and Coyle 1992).

My observations suggest that the cribellum and the calamistrum are not yet developed in first-instar spiderlings. The absence of these organs in first-instar individuals has also been observed in social spiders. For example, spiderlings of the colonial spider *Philoponella oweni* (Uloboridae) have no functional cribellum at the time of emergence (Eberhard 1977, Smith 1997), and they produce only ecribellate silk, so spiderlings' webs are not similar at all to adult webs (Smith 1997). In the subsequent instar, the cribellum of *P. oweni* is functional (Smith 1997). In the permanently social spider, *Stegodyphus sarasinorum* (Eresidae), these organs develop only after the third or fourth molt (Bradoo 1972). My observations suggest that the first stage of life in *A. ferox* is distinguished from the following ones by the immaturity of structures involved in the survival of the spiderlings (in particular, those that affect their ability to capture prey). Thus, it seems evident that the young of first instar are dependent on their mother.

Maintenance of group cohesion among *A. ferox* spiderlings is an important characteristic of the social relationship among siblings during the subsocial period (see Kim and Horel 1998, Kim and Roland 2000, Kim et al. 2005ab). The young spontaneously formed

a compact group if they were not perturbed. This behavior was also observed in the clutches where the mother had been removed. Such grouping behavior is frequently observed in spiders, including typically solitary species (Buskirk 1981, Ramousse 1977). Group cohesion among siblings, along with the presence of a web and mutual tolerance, might constitute pre-adaptations to permanent sociality (Shear 1970, Horel et al. 1996, Plateaux-Quénu et al. 1997). Clearly further study of social cohesion in spiders is warranted, particularly with regard to the underlying mechanisms.

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