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Development of locomotion in a subsocial spider

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ABSTRACT

Following consumption of their mother, the subsocial spider *Amaurobius ferox* remain together, exhibiting distinctive behaviours in response to intruders into the natal nest. We examined the ontogeny and characteristics of locomotory behaviours in *A. ferox* during this post-maternal social period. Locomotion of the spiderlings, elicited by the introduction of a cricket larva into the natal web, fell into two categories: 'abrupt locomotion' (AL) and 'ordinary locomotion' (OL). AL involved rapid and linear movement, whereas OL involved slower motion, not necessarily in a straight line. Both types of locomotion varied with spiderling age. AL appeared for only a limited period of time whereas the frequency of OL increased linearly over time. AL occurred more collectively than OL: the percentage of participants in a bout of locomotion was $18.67 \pm 17.71\%$ vs. $10.22 \pm 9.33\%$. The collective tendency of AL increased up until the seventh day and then decreased, whereas that of OL progressively decreased. The direction of AL responses to the intruder did not vary over time; however, for OL, movements towards increased in frequency over time. Locomotory responses also varied with the intensity of intruder movement. Including transient behaviours, the chronology of different behaviours suggests that behavioural development in *A. ferox* involves maternal influences and weakens group cohesion and collective tendency.

1. Introduction

Although more than 99% of spiders are solitary carnivores, all begin their lives exhibiting gregarious behaviours in the natal nest for at least the first few days after eclosion (Kullmann, 1972; D'Andréa, 1987). In subsocial spiders, maternal care prolongs this period, during which siblings show mutual tolerance and group cohesion (Horel and Krafft, 1986). In most subsocial spiders species, juveniles do not capture prey without maternal help; rather, the mother captures prey and shares it with her young (Kullmann, 1972; D'Andréa, 1987; Gundermann et al., 1991; Strickman et al., 1997; Evans, 1998). We do not know much how such young spiders transition to capturing prey in their own way.

Females of the subsocial spider *Amaurobius ferox* (Araneae, Amaurobiidae) are consumed by their offspring, a behaviour known as matriphagy (Kim and Horel, 1998). The young remain in the natal nest for 3–4 weeks after the death of their mother and collectively capture prey (Tahiri et al., 1989; Kim et al., 2005b). This stage of their life history differs from that of other subsocial spiders, in which dispersal time strongly depends on the presence of the mother (see Ruttan, 1990; Gundermann et al., 1993).

The post-maternal social organisation of *A. ferox* provides an opportunity to investigate the mechanisms of social behaviour in spiderlings while controlling for potential effects of maternal presence. The social organisation of *A. ferox* is intermediate between the maternal social stage of subsocial spiders and permanently social species. While inhabiting the maternal web, siblings commonly exhibit mutual tolerance and group cohesion (Horel et al., 1996; Plateaux-Quénu et al., 1997; Schneider, 2002). These behaviours are necessary precursors for the evolution of collective behaviour and permanent social organisation (Darwin, 1859; Crespi and Choe, 1997; Dugatkin, 1997).

At the onset of the post-maternal period, young are organised into a single instar homogenous group, with little variance in body mass among spiderlings (Kim et al., 2000; Kim and Roland, 2000; Kim, 2001). In contrast, individuals dispersing from the natal nest vary by developmental instar (i.e. third or fourth) and weight, with later-dispersing individuals weighing, on average, 3 times more than the first dispersers from the same clutch. Individual variation among spiderlings continues throughout the post-maternal period.

After matriphagy, *Amaurobius* spiderlings show very little activity. However, intruders, such as insects, into the maternal nest elicit strong reactions (Kim et al., 2005b; Kim, 2010). These reactions develop during the post-maternal period and can be divided into three categories: 'movement with body contraction', 'locomotion' and 'hunting'. The former category describes the movement of

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spiderlings accompanied by the contraction of their bodies. These contractions are triggered by the web vibrations intruders produce. Collectively, the contractions produce a strong pulsation of the entire web that could not be produced by a single individual (Kim, 2010). The movement with body contraction neither involves displacement nor orientation; it might be a collective defensive behaviour (Kim, 2010). Two or three days after the appearance of synchronised contractions, the spiderlings show distinctive locomotory behaviours, followed by predatory behaviours days later.

In this study, we examined the development and characteristics of locomotory behaviours in young individuals of the subsocial *A. ferox*. Young collectively show a very rapid and linear locomotion in a short distance in response to an intruder in the natal nest. Such a locomotory behaviour of the spiderlings resembles the successive synchronised stepping towards prey of the permanently social spider, *Anelosimus eximius* (Krafft and Pasquet, 1991; Vakanas and Krafft, 2001). We observed the development of different types of locomotion relative to the age of young, collective tendency (i.e. proportion of individuals within the clutch engaging in the behaviour), directional properties of the locomotion. We also investigated the reactions of young to the intensity of external stimuli. Little is known regarding the ontogeny of locomotion in subsocial spiders.

2. Methods

2.1. Natural history of the species

A. ferox Walckenaer (Araneae, Amaurobiidae) is a subsocial spider commonly found in Europe (Cloudsley-Thompson, 1955; Bristowe, 1958). Females spin irregular cribellate webs under stones in forest litter, in holes in old walls, and in other sheltered places (Cloudsley-Thompson, 1955; Tahiri et al., 1989). Maternal activity of *A. ferox* occurs in early summer and is characterised by caring behaviours performed over a fairly constant interval from the initiation of egg laying (Kim and Horel, 1998; Kim and Roland, 2000). After 20 days of incubation, 50–150 spiderlings emerge from the egg sac with maternal help (Kim, 2009a). One or two days after emergence, the mother provides her young trophic eggs, which are immediately consumed (Kim and Roland, 2000). Matriphagy occurs on the sixth day (5.7 ± 0.6 (mean $\pm$ SD) days) after emergence, i.e. one or two days after the first post-emergence moult is completed (4.1 ± 0.4 days after emergence; Kim, 2001) (Kim and Horel, 1998). *A. ferox* mothers are always devoured by their spiderlings, and all spiderlings within clutches benefit from the intake of their mother's body (Kim et al., 2000).

After their mother's death, the brood forms a temporary social group (Kullmann, 1972). Siblings remain in the natal nest for 3–4 weeks until dispersal (Kim, 2000). During this period, they pass through their second and third moults, occurring 12.2 ± 0.4 and 29.3 ± 1.4 days after emergence, respectively (Kim, 2001). Moults are highly synchronised within a clutch, and the low variance of moulting dates among clutches shows that these three moults occur on approximately the same dates after emergence (Kim, 2001). Two or three days after the second moult is complete, collective prey capturing appears (Kim et al., 2005b).

2.2. Collection and rearing

This study was carried out under laboratory conditions because they permitted clutch manipulations and because the preferred habitats of *A. ferox* preclude detailed observations in the field. Females were collected from early May to early June (i.e. before the egg laying period) from under stones and within damaged walls in the forested area of Nancy, France (northeastern France; 48°41′N, 6°13′E; elevation = 217 m; annual temperature = 9.6 ± 6.3 °C; annual precipitation = 74 cm).

Following collection, females were transferred to a closed room with fluorescent lighting (approximately 100 lux, 12:12 h light–dark cycle) and a temperature of 20 (± 2)°C. Females were individually placed in glass terrariums ($L = 200$, $W = 120$, $H = 200$ mm) partially filled with a mixture of sand and peat (Tahiri et al., 1989; Gundermann et al., 1993). The terrarium was humidified twice a week. Spiders were fed cricket larvae ad libitum. Laboratory experiments were conducted at the Laboratoire de Biologie et Physiologie du Comportement, Université Henri Poincaré – Nancy 1, France.

2.3. Behavioural observations

To investigate the ontogeny and characteristics of locomotory behaviour, we observed spiderlings remaining within the maternal web. The experiments ran from the third to the eleventh day after matriphagy, because spontaneous locomotion was commonly observed on the second or third day after matriphagy. For each trial, we introduced a cricket larva (*Gryllus bimaculatus*) onto the web to elicit spiderling movement. After matriphagy, the mean body mass of a single spiderling was 2.3 ± 0.2 mg (based on the measurement of five individuals within each of 12 clutches), whereas the mean body mass of the cricket larva was 20 ± 2 mg. A cricket larva of this size could be a potential predator for individual spiderlings or alternatively, a prey item for a group of spiderlings (see Kim et al., 2005a). Spiderling behaviours were video-recorded for 10 min upon introduction of the cricket. Observations and video recording were conducted daily from the third to the eleventh day after matriphagy.

2.4. Behavioural analysis

Quantitative data were collected from the videos of 10, 15, 16, 18, 14, 13, 10, 13 and 10 clutches on the 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th and 11th days after matriphagy, respectively, although observations were conducted on 20 clutches. Therefore, a total of 119 video sequences of 10 min each were examined. The smaller sample sizes for the quantitative data reflect problems with recording quality and the dispersal of young from the natal nest (Kim, 2000).

To obtain additional measures of individual behaviours, we used Etho Vision XT (Noldus Information Technology) to obtain measures of velocity, distance and time from the videos.

Measurements from the video images did not include all individuals within a group because the behaviours of the three-dimensional group were analysed using two-dimensional images. However, they allowed such a means of quantifying and analysing behaviour. The average number of individuals recorded on video images was 25.50 ± 12.29 ($n = 119$) and did not differ among days (Kruskal–Wallis test: $H_8 = 12.57$, $p = 0.1275$).

Ontogeny of behaviour: In the ten-minute video sequence initiated upon the introduction of the cricket to the web, we calculated the number of locomotory behaviours each individual conducted. We then calculated the average number of behaviours per individual over the 10 min.

Collective tendency: We calculated the proportion of individuals within each group that participated in each bout of locomotion. This proportion was calculated each day from the third to the eleventh day after matriphagy.

Direction of the behaviour: We classified the direction of locomotory behaviour relative to the cricket into three categories: (1) 'facing' (i.e. the individual oriented towards the cricket, (2) 'away' (i.e. the individual oriented away from the cricket), and (3) 'other' (i.e. when it oriented in any direction other than 'facing' and 'away'.