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Early experience and social performance in spiderlings

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The social context experienced during early ontogeny can have lifelong consequences on the expression of social skills, and social isolation during development frequently impairs social competence. In this study, we used spiders as a model to investigate whether early social experience shapes social performance later in life. In spiders, the juveniles of all species show a transient gregarious phase that extends after their emergence from the maternal cocoon and ends with the initiation of agonistic interactions and cannibalism. Most studies that investigated social interactions in spiderlings focused on kin recognition. However, the potential mechanisms shaping recognition and discrimination, and particularly the role of early social experience, received little attention. Therefore, we examined to what extent early social isolation can influence the expression of social behaviours. We also investigated the influence of familiarity and kinship, and of their interaction with social experience on the expression of cannibalism. Our results showed that social isolation of spiderlings of *Agelena labyrinthica* since the egg stage did not influence social performance after emergence. Our study advocates for the existence of a species-specific chemical signature inhibiting cannibalistic tendencies in spiderlings.

Social competence has been defined as the ability of individuals to optimize the expression of their social behaviours depending on available social information (Taborsky & Oliveira, 2012). Social competence requires individuals to process social information correctly and to display appropriate behavioural response to cues provided by conspecifics (Taborsky, Arnold, Junker, & Tschopp, 2012). Among the factors shaping social competence, the social environment experienced during ontogeny can have lifelong consequences on the expression of social skills. In several taxa, social competence is dependent on interactions with conspecifics during early development, and social isolation frequently results in an impairment of social performance at later ontogenic stages (Bekoff, 1972; Scott, 1962; Toth, Mikics, Tulogdi, Aliczki, & Haller, 2011). In *Drosophila* for instance, visual attraction to larvae is a learned trait that requires an exposure to moving larvae during a developmental critical period (Slepian et al., 2015). In zebra finches, *Taeniopygia guttata*, the social context encountered during adolescence influences social integration and grouping behaviours later in life (Ruploh, Bischof, & von Engelhardt, 2014). Similarly, juveniles of the cichlid fish *Pelvicachromis taeniatus* reared in isolation are more aggressive and less prone to shoal than group-reared conspecifics (Hesse & Thünken, 2014). Most work investigating the influence of early social context on social competence focused on vertebrates (e.g. Kaiser & Sachser, 2005), but little is known about how early social environment shapes social performance in arthropods.

Spiders are ideal models to study the mechanisms underlying the ontogenesis and expression of social performance. The vast majority of spiders are solitary and aggressive at adulthood (Wise, 2006). However, the ontogeny of all species of spiders is characterized by a transient gregarious phase during the initial developmental stages (Horel, Krafft, & Aron, 1996). The duration of this gregarious phase is highly variable across species and terminates progressively by a lessening in the strength of attraction between juveniles and the onset of aggressive interactions (Mougenot, Combe, & Jeanson, 2012). Most work on the expression of social behaviours in spiderlings examined whether they preferentially cannibalize siblings or nonsiblings. The evidence of kin recognition documented in several species (*Australomisidia ergandros* (=*Diaea ergandros*): Evans, 1998, 1999; *Stegodyphus lineatus*: Bilde & Lubin, 2001; *Delena cancerides*: Beavis, Rowell, & Evans, 2007; *Hogna*

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helluo: Roberts, Taylor, & Uetz, 2003) contrasts with the absence of kin recognition reported in others (e.g. *Geolycosa turricola*: Miller, 1989; *Misumena vatia*: Morse, 2011; *Pardosa amentata*: Hvam, Mayntz, & Nielsen, 2005; *Pardosa palustris*: Rickers & Scheu, 2005). Importantly, the general trend reported in these studies reveals a reluctance to cannibalize conspecifics before the dispersal stage. Strong reluctance for cannibalism in spiderlings, despite low energetic stores and the ability to subdue prey (Lesne, Trabalon, & Jeanson, 2016), advocates for the existence of specific processes that inhibit the onset of aggression between conspecifics. One such process could rely on the development of social recognition mechanisms prior to emerging from the cocoon. In spiders, an exposure to siblings during a critical period in the maternal cocoon could thus represent a mechanism by which juveniles could learn the phenotypic cues of conspecific spiderlings. However, this hypothesis has never been tested, and it is not yet known whether early social interactions experienced by hatchlings play a role in shaping social performance in spiderlings. To our knowledge, only one study so far examined the influence of early social contacts on the propensity to cannibalize conspecifics in arachnids. In the mite *Phytoseiulus persimilis*, individuals reared in isolation cannibalize more siblings than nonsiblings while the reverse pattern was found for nymphs that experienced social contacts during early development (Schausberger, 2004). This study however involved individuals of different development stages (protonymphs and larvae as cannibals and prey, respectively).

Here, we proposed to investigate whether social performance in spiderlings is innate or involves learning. We tested whether early social experience before emergence from the maternal cocoon shapes the nature of the very first social interactions and plays a role in the expression of social behaviours in spiderlings of the solitary species *Agelena labyrinthica*. Socially experienced spiderlings were reared with a conspecific from the egg stage whereas socially deprived individuals were isolated before egg hatching to prevent the acquisition of any conspecific cue via social interactions. If early contacts with conspecifics reduce the expression of agonistic behaviours, we predicted that spiderlings reared in isolation since the egg stage should show less tolerant behaviours and a higher level of cannibalism than juveniles that experienced early social interactions. In addition, spiderlings with or without early social experience were paired with a conspecific that differed in familiarity and/or kinship. This design thus also allowed us to investigate the influence of these two attributes, and their interaction with social experience, on social performance.

METHODS

Biological Model

Agelena labyrinthica (Agelenidae, Clerck 1758) is a solitary web-building spider widely distributed in southern and central Europe. Females usually lay one to three cocoons containing 50–130 eggs in late summer. Hatching occurs inside the cocoon after a period of incubation of about 20 days. At this stage, larvae show little mobility and get their nutrients from egg yolk. This first instar lasts 1 week and ends with a first moult, which occurs inside the cocoon and leads to the emergence of fully mobile individuals (second instar). Spiderlings then enter a winter diapause that lasts until early spring when they emerge from the maternal cocoon and remain gregarious for a few days prior dispersal (Mougenot et al., 2012). Second-instar spiderlings are mobile, produce silk and display hunting behaviours toward prey (Lesne & Jeanson, 2015).

In total, we collected 36 cocoons at two sites approximately 190 km apart: Gilet (Gironde, France, GPS: 44°46′59.6″N, 0°13′39.1″E) on 7 August 2014 ($N = 18$) and Lacaugne (Haute-Garonne, France, GPS: 43°17′15.0″N, 1°16′05.6″E) on 21 August 2014 ($N = 18$). Within a site, cocoons were within 200 m of each other.

Experimental Groups

We defined two developmental phases: the pre-emergence phase, which spans from the hatching of eggs to the end of winter diapause, and the post-emergence phase, which follows the winter diapause. The experimental manipulations during the pre-emergence phase allowed us to modify the early social context. The manipulations during the post-emergence phase enabled to test the influence of early social context while controlling for the potential confounding effects of familiarity and kinship (see below).

Pre-emergence phase

Upon collection in the field, cocoons were gently opened with callipers before the hatching of eggs. Eggs were haphazardly assigned to one of four treatments: (1) a single egg was placed in a microtube ($N = 420$); (2) two eggs from the same cocoon were placed in the same microtube ($N = 210$); (3) one egg from two different cocoons collected at the same site were placed together in the same microtube ($N = 210$); or (4) one egg from two cocoons collected at the two different sites were placed together in the same microtube ($N = 210$) (Fig. 1, single tubes above the white dotted line).

The microtubes (Axygen®, 0.6 ml) were closed by a humidified filter (Rizla+®, length: 15 mm, diameter: 6 mm) to allow gas exchanges. Eggs hatched between 26 August and 7 September 2014 (11% of eggs never hatched). Spiderlings began their first moult between 1 and 13 September 2014 (3.5% of hatchlings died before or during their first moult). After their first moult, second-instar spiderlings were maintained at ambient temperature (25 °C) during 10 days and were then placed at 4 °C in a cooled room under a 8:16 h light:dark cycle to simulate winter diapause. No spider died during diapause. We terminated diapause on 12 November 2014 and placed all tubes at ambient temperature (25 °C).

Post-emergence phase

We formed nine experimental groups of pairs of second-instar spiderlings differing in their social experience, familiarity and kinship (Fig. 1). We considered that spiderlings had social experience (S^+, Fig. 1) if they were paired with a conspecific during the pre-emergence phase (i.e. from the egg stage to the end of the diapause). Two individuals were considered familiar if they were together during the pre-emergence phase (F^+, Fig. 1). Finally, spiderlings within pairs differed in kinship. We assumed that kinship was maximal between individuals from the same cocoon (K^+, Fig. 1), minimal between spiderlings from cocoons collected at two distant sites (K^-, Fig. 1) and intermediate for juveniles from different cocoons collected within a site (K^0, Fig. 1). We considered nine different combinations. This design represents the exhaustive number of possible combinations, as it is not feasible to combine familiarity with an absence of social experience (i.e. F^+S^-). For each combination, 35 pairs were formed by selecting randomly among the individuals from the pre-emergence manipulation, for a total of 315 pairs.

Behavioural Tests

Early hunting ability

This experiment aimed to control for the ability of spiderlings to display predatory behaviour in the early days following their emergence from the cocoon. Spiderlings were introduced individually into experimental arenas with a *Drosophila*. Each arena consisted in a transparent petri dish lid (diameter: 5.5 cm, height: 0.9 cm) placed on a piece of drywall (Placoplâtre®) soaked in water.