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Maternal care and reproductive state-dependent mobility determine natal dispersal in a wolf spider

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By facilitating avoidance of kin competition and inbreeding, natal dispersal can have direct fitness consequences. Mechanisms that optimize indirect fitness may be equally important. When relatives compete for the same resources (kin competition), evolution of elevated dispersal rates can be favoured, so that most resource competition is among nonrelatives. When offspring are incapable of dispersing, maternal behaviour may influence natal dispersal in a positive way, by spreading offspring throughout the habitat. By combining laboratory and field observations, we studied dismounting behaviour of spiderlings from the maternal abdomen (i.e. maternal care) and mobility patterns of female wolf spiders, *Pardosa monticola*. Laboratory observations on the duration of maternal care indicated that spiderlings desert the maternal abdomen gradually within 185 h of hatching. Detailed behavioural monitoring within the spider's habitat showed that females carrying spiderlings on their back were more mobile with greater directionality of movement than females of other reproductive states. This alteration in female mobility, together with the gradual dismounting of offspring from the abdomen, indicates maternally induced natal 'hitchhiking' dispersal. These findings show that maternal effects may influence natal dispersal not only through condition dependence, but also by the active spreading of offspring throughout the habitat before they actively (decide to) disperse. This gradual dismounting of offspring is evolutionarily beneficial for the avoidance of kin competition.

Keywords: maternal care; mobility; natal dispersal; *Pardosa monticola*; wolf spider

Natal dispersal in animals has been hypothesized to be either a mechanism to avoid kin competition (e.g. Hamilton & May 1977; Kasuya 2000; Perrin & Lehman 2001), or inbreeding (e.g. Pusey 1987; Gandon 1999) or a bet-hedging strategy in unpredictable, spatially heterogeneous habitat (e.g. Hopper 1999; Mathias et al. 2001; Toonen & Pawlick 2001). These factors affect dispersal not only because of their direct fitness consequences, but also because of indirect ones, that is, when there are benefits (kin altruism) or costs (kin competition) to relatives within a group. When relatives compete for the same resources (kin competition), dispersal rates are predicted to be high (e.g. Gandon 1999; Kisdi 2004; Bach et al. 2006), so that most resource competition is among nonrelatives (Kasuya 2000; Ridley & Sutherland 2002). As well as direct kin interactions, the avoidance of inbreeding may also contribute to elevated dispersal rates (Gandon 1999; Perrin & Mazalov 1999; Bilde et al. 2005). Only when the costs of dispersal (e.g. energetic costs, high mortality probabilities) are greater than the costs related to inbreeding depression (Waser et al. 1986) or kin competition (Bach et al. 2006), is dispersal not evolutionarily beneficial. Besides these ultimate factors, proximate mechanisms, such as behavioural responses to changes in environmental conditions, are known to underlie natal dispersal (Massot & Clobert 2000). For arthropods in general, deteriorating habitat conditions

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accompanied by scarcity of resources (Morse 1993; Bonte et al. 2003b; Van Dyck & Baguette 2005), (over-)crowded conditions (Enfjäll & Leimar 2005) and the presence of predators (Harrison 1997) are the best known environmental triggers.

Dispersal is also known to be environmentally determined through changes in 'internal' state (Ims & Hjermann 2001), which can occur in the prenatal phase (Massot & Clobert 2000) through maternal effects (Merilä & Svensson 1997). These maternal effects on dispersal are especially important if offspring are not capable of directly perceiving cues from the external environment or of assessing kinship during early juvenile development. Under such conditions, mothers may indirectly convey information about the environment to dispersing offspring (Ims & Hjermann 2001). An obvious, although scarcely addressed, maternal influence comprises the selection of natal habitat as a function of the social environment (Lena et al. 2000), local population structure (Ims 1990; Hanski et al. 1991) and habitat quality (Morse 1993; Diss et al. 1996). Especially in arthropods that lay eggs in clusters and have fairly sedentary offspring, early natal dispersal may be important for avoiding both competition among kin for suitable microhabitats and resources (Morse 1993) and cannibalism (Vanden Borre et al. 2006). When offspring are unable to disperse, maternal behaviour may influence natal dispersal directly (Dingemanse et al. 2003), by an active spreading of offspring throughout the habitat.

Wolf spiders (Araneae, Lycosidae) are among the most dominant predatory arthropods in terrestrial ecosystems and in grasslands in particular (Foelix 1996). Instead of residing within webs, they have adopted a wandering foraging behaviour that varies between a sit-and-wait strategy in juveniles and a vagile strategy in adults (Samu et al. 2003). Inter- and intraspecific variation in foraging strategy occurs in relation to general life history (e.g. burrowing lifestyle), habitat structure, hunger state and gender (Morse 1997; Walker et al. 1999; Samu et al. 2003; Bonte et al. 2004). Typically, wolf spider females show maternal care and carry their eggsac attached to their spinnerets; after hatching, the spiderlings climb on their mother's back, despite their ability to run and feed independently (Foelix 1996) and are transported for a certain period. Once spiderlings leave the female's abdomen, they do not climb back on to it (D. Bonte & S. Van Belle, unpublished data). Although not documented in the literature, females carrying spiderlings actively forage and attack prey (S. Van Belle, D. Bonte & J.-P. Maelfait, unpublished data). Currently, the advantages of this maternal care are not known. Spiderlings do not feed on the abdomen, are not fed by the mother (as in e.g. Eresidae, Agelenidae; Foelix 1996; Salomon et al. 2005) and rely on earlier eggsac reserves for survival (Foelix 1996). Because the first free-living instars defend 'mobile territories' and show low levels of cursorial and ballooning mobility (Richter et al. 1971; Bonte et al. 2006), strong kin competition for both food and suitable microhabitat is predicted if spiderlings leave the maternal abdomen simultaneously (i.e. at the same location).

Females are predicted to have an active foraging strategy during periods of internal egg development when energy demands are high (Uetz 1992; Wise 1993) and more passive 'sit-and-wait' strategies after egg production. Females carrying eggsacs are predicted to be particularly sedentary because of the need for constant and optimal temperature conditions for egg development within the attached eggsacs (Devito & Formanowicz 2003). After hatching, however, mobility is expected to increase since females develop a second eggsac and so have high energy demands. They may also increase foraging activities to compensate for the previous period of immobility in which they presumably starved. As a result, if females become more active when carrying spiderlings, future kin competition could be avoided by the spiderlings leaving at different times. Since this reduction in future kin competition for resources and space is evolutionarily beneficial, increased female activity and asynchronous abdominal desertion rates of spiderlings may alternatively originate by natural selection.

In the light of these predictions, we studied mobility patterns and maternal care in the wolf spider *Pardosa monticola* in field and laboratory observations. In the Flemish coastal dunes, the species lives in short dune grasslands (Bonte & Maelfait 2001) and shows only negligible juvenile ballooning dispersal in later instars under extreme starvation (Bonte & Maelfait 2001; Bonte et al. 2006). The food of early instars is locally aggregated depending on soil and vegetation properties (Bonte & Mertens 2003). Juvenile cannibalism is common because spiderlings show similar microhabitat preferences within local subpopulations (Vanden Borre et al. 2006). Because of expected severe kin competition caused by low active juvenile dispersal (both wandering and ballooning), strongly aggregated prey and high cannibalism rates in early instars, we hypothesized that spiderlings should disperse at different times and places within the habitat.

METHODS

Duration of Maternal Care

We collected spiders form the 'Westhoek' dune reserve, De Panne, Belgium, on 29 June 2005. Females ($N = 52$) with attached eggsacs were kept in the laboratory at 22°C in terraria (diameter 9 cm) with plaster of Paris to maintain sufficient humidity. All females were checked at least twice a day (morning and evening) for hatching of the eggs. We noted the time of hatching and the number of spiderlings that had left the maternal abdomen. From the moment all spiderlings had left the maternal abdomen, mother spiders and their offspring were preserved in 70% ethanol for size determination. We could thus count the spiderlings that were initially on the female's abdomen (brood size). To determine the size of females and spiderlings we measured cephalothorax width under a binocular microscope.

Mobility

We studied mobility patterns of *P. monticola* in coastal dune grasslands of the Westhoek nature reserve of De Panne, Belgium. Observations were made during the activity period of adult females (June–August 2005). Because