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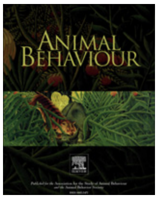

Selective integration advantages when transience is costly: immigration behaviour in an agrobiont spider

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Dispersal, and especially movement between the natal and the new environment, is a costly process. Costs are incurred not only during the preparation or transfer phase but also on arrival in a new environment. Such costs comprise, for instance, time costs because of the need to search for a suitable microhabitat or integration costs when immigration occurs in already densely populated habitat. The failure to settle or to integrate may consequently inflate the costs already incurred during emigration and transfer. Therefore, we expect emigrating individuals to have evolved enhanced integration capacities. In our laboratory experiments, dispersive phenotypes of the agrobiont spider *Erigone atra* were characterized by (1) faster settlement in empty habitat and (2) increased willingness to compete for ownership of already occupied sites. These correlated behaviours point to dispersive phenotypes (1) being likely to experience a selective advantage at settlement and (2) not being a random subsample from the population. These correlated behaviours are predicted to have a strong impact on spatial population dynamics and gene flow.

Understanding the causes and consequences of dispersal is fundamental to understanding ecological and evolutionary patterns in modern spatial ecology (Kokko & Lopez-Sepulcre 2006). Instead of considering dispersal solely as the movement of organisms away from their natal habitat, it has become clear that dispersal should be regarded as a three-stage life history trait including emigration, transfer and immigration (Clobert et al. 2009) and that life history variation during each of these stages may impact on how far or how often individuals move away from their place of birth (Benard & McCauley 2008). Splitting dispersal into different stages will therefore allow a better understanding of how fitness costs are incurred at each stage and how this affects selection on particular aspects of the dispersal strategy. It implies, however, that we need to understand how fitness costs at one stage feed back to the costs and benefits at another stage.

To date, the main costs of dispersal are believed to be those associated with emigration and/or transfer (Clobert et al. 2009). Costs of dispersal, however, are not incurred equally by all individuals from a population. Individuals in better body condition may, for instance, experience lower levels of predation pressure or simply use less energy during transfer (King & Roff 2010). The fitness of established dispersers (Lin & Batzli 2004) should therefore only be equal to that of the residents when dispersal is completely free of costs.

Dispersal evolves as an alternative strategy to philopatry such that these two behavioural strategies have equal fitness, resulting in a mixed evolutionarily stable strategy (Maynard Smith 1982). When costs of dispersal become prevalent in one of the three defined dispersal stages, the resident fitness hypothesis (Hamilton & May 1977) predicts that the realized fitness of emigrants should be lower than that of residents if they are forced out of the population to decrease local competition. This is better known as the social dominance hypothesis (Fretwell 1972). Alternatively, the cost of dispersal hypothesis (Morris 1987) predicts that, because dispersal is costly, individuals should leave home in favour of an alternative habitat only when potential fitness in the alternative exceeds that in the current habitat by a value greater than the cost of emigration and transfer.

If certain phenotypes within a population are able to deal better with the costs of finding free habitat relative to others, they are expected to benefit most by moving away (Hanski et al. 2006; Saastamoinen 2007a; Bonte et al. 2009, 2008; Amarasekare

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2010). However, when new habitat is not vacant or is populated at carrying capacity, integration can be seriously hampered by intraspecific competition for space and food. Under these circumstances, an increased ability to take over suitable habitat from residents will benefit immigrants and reduce the entire cost of the dispersal process. In phenotypically heterogeneous populations, this advantage is, for instance, hypothesized to be driven by changes in the local natal or maternal conditions that increase body condition, and is referred to as 'silver spoons' (Stamps 2006).

Because integration failure may inflate the costs already incurred during transfer and emigration, the cost of the entire dispersal process can be reduced if immigrants consist of those individuals from a population with characteristics that facilitate integration in novel environments. This process may be common in both kin-structured populations (Gyllenberg et al. 2008) and non-kin-structured populations (Cote et al. 2008; Fraser et al. 2001) and will eventually balance costs and benefits between philopatric individuals that do not incur any costs of moving away and dispersive individuals that both incur the costs and reap the benefits of dispersal.

In spiders, dispersal is mediated by distinct behaviours preceding transfer. By means of tiptoe behaviour (i.e. stretching the legs, raising the abdomen and producing silk threads) spiders initiate long-distance dispersal by which they are transported attached to silk threads in the air (this is called ballooning). They may alternatively move short distances by using silk threads as bridges (rappelling). Owing to mechanistic constraints, ballooning is restricted to smaller individuals, such as adults of smaller money spiders (Linyphiidae) or juveniles of larger families such as wolf spiders (Lycosidae). In the latter, routine cursorial movements (Bonte et al. 2004) and maternally assisted spreading of offspring (Bonte et al. 2007) also exist as adult and natal dispersal mechanisms, respectively. Obviously, the different dispersal modes largely differ in efficiency and underlying cost structure. In the case of ballooning, costs are directly related to the availability of suitable habitat within the dispersal perimeter (with area-scaled costs; Englund & Hamback 2007). Spiders climb elevated structures in the vegetation to prepare for take-off (producing silk lines that are used as an airborne sail; Bell et al. 2005). By doing so, they expose themselves to predators and experience mortality or damage costs before and during the emigration preparation phase (Young & Lockley 1988). Besides the energetic investment for positioning (climbing up the vegetation), the production of silk lines is also intrinsically costly (Bell et al. 2005). Of the two silk-assisted dispersal modes, ballooning is the only consistent behaviour. Repeatability has been found to be within the range of 0.4–0.6 in the agrobiont spider *Erigone atra* (Bonte et al. 2009); heritability estimates for ballooning were found to be within the range of 0.17–0.42 in a wolf spider and in *E. atra*, but were largely dependent on the prevailing environmental conditions (Bonte et al. 2003; Bonte & Lens 2007). This allows us to identify the ballooning phenotype based on simple experimental assays. We refer to this behavioural type as the dispersive phenotype and to those not showing this behaviour as the philopatric phenotype. Moreover, earlier research showed that dispersive phenotypes are in better general body condition, as reflected by the positive correlation with longevity and reproduction (Bonte et al. 2008).

Because the costs of ballooning are inevitably high during the preparation and transfer phase, we hypothesized that those individuals performing ballooning may experience reduced immigration costs because of their generally better body condition. We tested this hypothesis using *E. atra* as a model. This species experiences two dispersal windows in its natural environment: one dispersal event in spring in which earlier sown crops are colonized, and one mass dispersal event in late summer when the spiders abandon the crops. During spring dispersal, the species is expected to have limited time to find suitable microhabitat for settlement. We therefore predicted that dispersive phenotypes would select suitable microsites faster than their philopatric counterparts to reduce time costs. In late summer and autumn, however, dispersing individuals need to settle in overcrowded habitat for hibernation. These hibernation sites comprise small elements of natural vegetation such as crop verges where immigrating spiders encounter high densities of conspecifics (Sunderland & Samu 2000). Dispersive phenotypes should therefore be more committed to compete for and to take over already occupied microhabitat. We tested these hypotheses under laboratory conditions by comparing behaviour related to microhabitat selection and web take-over between dispersive and philopatric phenotypes of *E. atra*.

METHODS

Study Species

Erigone atra is an abundant, small (3–5 mm) sheetweb spider inhabiting crops sown during autumn (Downie et al. 2000) and one of the commonest aeronautically dispersing spiders in Western Europe (Bell et al. 2005). As in other Linyphiid spiders, adult individuals engage in aerial dispersal by ballooning. In contrast to other movement behaviours in this species, ballooning is a consistent and heritable behaviour (Bonte et al. 2003, 2009). Females occupy small cavities in the soil as suitable microhabitat for web building and remain there for foraging. We reared spiders at similar densities (20 individuals) in large containers measuring 25×15 cm^2 with prey (Collembola: *Sinella curviseta*) ad libitum. Ballooning dispersal was found to be independent of density during development, but triggered by the presence of silk on take-off platforms (De Meester & Bonte 2010). The size of a subset of the individuals tested for dispersal phenotype was determined by measuring cephalothorax width under a binocular microscope.

Assessment of the Dispersal Phenotype

Individual dispersal motivation was quantified using previously established protocols (see Bonte et al. 2008, 2009) in a wind tunnel with upward wind currents of 1 ± 0.2 m/s, reflecting optimal conditions for aerial dispersal. During 10 min, a time span considered to provide a representative picture of the dispersal capacities of the spider, we recorded the individual's motivation to engage in ballooning. Only individuals that effectively took off were regarded as ballooners; those that remained on the platform or only engaged in short-distance rappelling movements were considered to be philopatric individuals.

Experimental Set-up

Experiment 1: time to settle (search strategy)

We designed a set of plastic arenas (10×10 cm^2) with plaster of Paris on the bottom. Within each arena, one cavity with a diameter of 4 cm and depth of 2 cm was created in the plaster as a microsite for web building. The cavity was filled with a fruit medium to attract released prey (fruit flies, *Drosophila melanogaster*). In each arena, one female (either a dispersive or philopatric phenotype tested the same day) was released and the time to the start of web building was recorded. A total of 63 females (30 dispersive and 33 philopatric phenotypes) were tested. The experiment was finished when all the females had built a web above the cavity in their arena (all less than 5 h).