Dispersal syndromes in butterflies and spiders

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13.1 Introduction

Dispersal is essential for the persistence of populations in fragmented landscapes (Chapters 20, 30, 31, 34), and can play a key role in determining the range expansion dynamics of invasive species and range-shifting in response to climate change (Chapter 26). Dispersal is an expensive life-history trait with costs imposed during dispersal itself, but often also during other stages of the life history (Bonte et al. 2012). The selection pressures on dispersal and related life-history traits are likely to vary across species and among individuals within a species. In addition to natural selection affecting dispersal phenotypes, environmental conditions during development and during the actual dispersal process may further shape individual phenotypes with covarying dispersal-related life-history traits (Chapter 10). Understanding the evolution of dispersal therefore requires an understanding of the way dispersal influences, and is influenced by, the behavioural and/or life-history traits that are associated with it. The covariation of life-history traits with dispersal defines a dispersal syndrome; i.e. dispersers may be similar in behaviour, morphology, and life history compared with nondispersers. These dispersal-life history correlates have been traditionally studied in wing-dimorphic insects like crickets and bugs. In these species, polymorphism in wing and flight muscle development (pterygomorphism) is correlated with various life-history traits both within- and among species. In the herbivorous Dysdericus beetles, species from ephemeral habitats allocate resources into dispersal (wings and flight muscles) during development while delaying maturity and reproduction (oögenesis-flight syndrome). This trade-off is evident even though dispersive individuals are able to re-allocate resources from flight muscles (histolysis) back to reproduction after settlement (Derr *et al.* 1981; Harrison 1980). Similarly, within species, Roff and colleagues have demonstrated that life-history traits between winged and wingless cricket morphs mostly show negative covariation (Roff and DeRose 2001; Roff *et al.* 2002; Roff *et al.* 1999; Stirling *et al.* 2001). These negative correlations have been shown to be mediated through changes in hormone titres, feeding back on basal metabolism (Zera and Bottsford 2001; Zera and Mole 1994; Zera *et al.* 1994).

Alongside the large body of literature focusing on distinctive wing polymorphisms, we here aim to focus on arthropods with dispersal as a continuous, behaviourally mediated trait. Our aim is to discuss covariation of dispersal with other life-history traits in two groups (spiders and butterflies) which have no obvious morphological dispersal adaptations. As we will show here, dispersive phenotypes show strong phenotypic correlates with other life-history traits, and these correlations are often shaped by environmental conditions experienced during dispersal itself, during the life stages immediately preceding emigration, during the natal development, and even conditions experienced by previous generations. The correlated responses are therefore context-specific and highly depending on the scale of biological organization. Here, the focus will be on between- and within-population comparisons rather than on comparisons between species.

13.2 Dispersal syndromes among populations: the Glanville fritillary system as an example of butterfly with a colonizer syndrome

In butterflies, dispersal relies on flight ability, which is also a fundamental prerequisite for other life-history functions, as individuals need to fly in order to forage, locate mating partners, and distribute eggs. Even though there are examples of both between (Stevens et al. 2010) and within-species (Hill et al. 1999; Thomas et al. 2001) that indicate how in some cases flight-related morphological traits are reliable proxies of dispersal, it is currently debatable how much interpatch movements depend on special behaviours rather than routine movements (Van Dyck and Baguette 2005). In the butterfly case study discussed here we have consistently showed that dispersal and flight-related components, such as within-patch mobility (Hanski et al. 2006) and flight metabolic rate (Niitepõld et al. 2009), are linked (for more details, see Case Study III and Chapter 23). In addition, variation in dispersal ability is tightly linked to variation in one gene, Pgi, encoding a glycolytic enzyme Phopshoglucose isomerase. Females with a particular genotype, Pgi-f, have higher peak flight metabolic rate, higher dispersal ability in the field, and this genotype is more frequent in the newly established populations (Haag et al. 2005). In contrast to females, males do not show similar positive correlation between dispersal and peak flight metabolic rate, presumably as high flight capacity in males is related to territorial behaviour and increases the number of matings, whereas inferior males may be those forced to disperse (Niitepõld et al. 2011). Thus flight capacity has opposite associations with dispersal rate in the two sexes, but as females are those that establish new populations, we will concentrate on them in Case Study III. Interestingly, however, there does not seem to be any significant differences in flight-related morphologies between the dispersive and non-dispersive individuals in either females or males.

As dispersal is energetically costly, correlations between dispersal and other life-history traits are often presumed to be negative simply because resources allocated to dispersal are no longer available for other energetically expensive traits. In accordance with this idea, in the speckled wood butterflies, for example, individuals from highly fragmented agricultural landscapes have reduced fecundity and lifespan relative to individuals from continuous woodland, due to the higher dispersal costs between suitable habitat fragments, and associated differences in flight morphology and behaviour (Gibbs and Van Dyck 2010). In this species, increased dispersal is associated with reduced investment in reproduction in populations that are expanding their range, and which possess higher dispersal rates than populations at the core of the range (e.g., Hughes et al. 2003). A contrasting dispersal syndrome is that of a 'colonizer syndrome', in which highly dispersive and / or mobile individuals show rapid development, early reproduction and high fecundity (Baker and Stebbins 1965). Individuals showing such positive correlations, between flight ability and other life-history traits, have also been called 'super dispersers' or 'fugitive species' (Hutchinson 1951). A positive correlation between dispersal and reproduction in dispersive species or populations has been explained by the selective advantage of such correlation due to increased success of individuals colonizing new habitats (Dingle et al. 1988; Ritte 1978; Chapter 10). Following, we will discuss in more detail an example of the colonizer syndrome in a butterfly case study.

The Glanville fritillary butterfly occurs in a highly fragmented landscape and has a classic metapopulation structure in the Åland Islands, south-west Finland (Hanski 1999), with a high rate of population turnover (extinctions and recolonizations; Nieminen et al. 2004). Hundreds of new populations are established each year on habitat patches that were unoccupied in the previous year, and these populations compensate for the loss of similar number of local population extinctions (Case Study III, and Chapter 23). Females establishing these new populations are more dispersive than females from already established old populations (populations that have existed for more than five years without going extinct; Hanski et al. 2002; Hanski et al. 2004; Chapter 23). This difference can simply be explained by females with high dispersal ability being more likely to successfully colonize new, habitat patches,

especially isolated ones. As dispersal has a genetic bases (Klemme and Hanski 2009; Saastamoinen and Hanski 2008; Saastamoinen 2008), the offspring of these females also have higher dispersal ability.

Based on numerous different studies on the Glanville fritillary butterfly, in which we have compared within-patch mobility of females from newly established and old populations, or females with different Pgi genotypes in large outdoor enclosures, our general conclusion is that there is no evident trade-off between dispersal and reproduction. Instead numerous fecundity-related lifehistory traits show positive correlation with dispersal ability (Table 13.1 and Figure 13.2). More mobile females initiate reproduction (mating and/ or oviposition) at younger age, and have higher mating frequency compared with the more sedentary females (Klemme and Hanski 2009; Saastamoinen 2007a; Saastamoinen 2007b, Figure 13.1). This may partially be due to the fact that females from newly established populations, which in general are also more mobile, mature eggs at faster rate than females from old populations (Wheat et al. in prep). Even though the potential fecundity, essentially the number of oocytes at eclosion, is lower in females from the newly established populations (Hanski et al. 2004), this tradeoff does not translate to difference in lifetime egg production (Saastamoinen 2007b). It seems that under field conditions, females only rarely are able to lay all the eggs they have at eclosion. In addition, females with a particular genotype, Pgi-f, lay on average, 20-30% larger clutches compared with females with the Pgi-d genotype (Saastamoinen 2007a; Saastamoinen and Hanski 2008). Given that *Pgi-f* genotype is related to higher flight metabolic rate, higher dispersal, and is found in higher frequencies in newly established than old populations, this difference actually suggests a positive correlation between dispersal and clutch size. The higher clutch size of the Pgi-f females is at least partially explained by Pgi-f females being able to fly at lower ambient temperatures and hence being active earlier in the day, and thereby initiating oviposition during the most favourable conditions in the early afternoon, which in general increases clutch size (Saastamoinen and Hanski 2008).

Even though *Pgi-f* females lay larger and more clutches, the lifetime egg production seems to be approximately equal in the two types of population (Saastamoinen 2007b). Interestingly, however, in newly established populations within-patch mobility is positively correlated with lifetime reproduc-

	Newly established populations	Old populations
Dispersal-related traits:		
Dispersal	high	low
Within-patch mobility	high	low
Flight metabolic rate	high	low
Most common Pgi-genotype	Pgi-f	Pgi-d
Life-history traits:		
Development time*	equal	equal
Body size	equal	equal
Egg maturation	high	low
Age at first reproduction	low	high
Number of oocytes	low	high
Clutch size*	high	low
Lifetime egg production	equal	equal
Lifespan	low under stressful conditions ¹	high under stressful conditions ¹

 Table 13.1
 Comparisons of dispersal and related life-history traits between newly established and old populations in the Glanville fritillary butterfly.

* based solely on comparisons between the Pgi-genotypes.¹ under laboratory conditions individuals with Pgi-f genotype live longer. tive success, whereas in old populations the opposite is true, and more mobile females have reduced lifetime egg production compared with sedentary females (Saastamoinen 2007b). These results are reminiscent of some previous results comparing dispersive versus sedentary species/populations (Lavie and Ritte 1978; Wu 1981), and have been suggested to indicate dissimilar selection on dispersal and related life-history traits between newly established and old populations. The positive correlation between dispersal and fitness (i.e. the colonizer syndrome) especially in the newly established isolated population is in general assumed to be characteristic for species frequently colonizing ephemeral habitats and hence living in highly unstable habitats (Rankin and Burchsted 1992; Ronce and Olivieri 2004). On the other hand, for individuals living in more permanent (i.e. old) populations, high dispersal rate is not so essential and in such cases selection is thought to favour individuals with other fecundity-related life-history traits, for instance increased longevity (Chapter 23).

Comparisons of individual life-history traits in M. cinxia between old and new populations in enclosures suggested that individuals from newly established populations have a shorter lifespan than females from established populations (Hanski et al. 2006; Zheng et al. 2007). This would imply that the new population females have a so-called 'fast' life-history strategy; they initiate oviposition at young age, produce larger clutches at faster rate but have a shorter lifespan. Equivalent lifetime egg production is achieved by females from old populations, but these females, who move less, seem to compensate for the slower reproduction by longer lifespan. Laboratory studies, conducted under constant optimal environmental conditions, have, however, shown that the story is more complicated, as females with Pgi-f genotype, which is more frequent in the new populations, actually live longer than females without this genotype (Klemme and Hanski 2009; Saastamoinen et al. 2009). Taken together, the often significant but conflicting results on differences in lifespan under different experimental conditions suggest that the effect of genotype and time since the population was established are highly dependent on the environmental condi-

tions. Possibly under unlimited food conditions in the laboratory, the more mobile individuals can increase food intake sufficiently to compensate for the energetic cost of higher mobility, whereas the trade-off between mobility and lifespan may be apparent under more restricted food availability under semi-natural conditions in the population enclosure. This hypothesis is also supported by the fact that the effect of the rate of reproduction on abdomen weight loss (indication of depletion of resources) is much greater in the *Pgi-f* than in the other genotypes (Saastamoinen et al. 2009). This suggests a trade-off between fecundity and maintenance, since if the Pgi-non-f females are able to reproduce with a smaller reduction of resources in the abdomen, it leaves more resource left for maintenance, potentially prolonging the lifespan under some conditions (e.g. mild food stress). As concluded by Reznick et al. (2000), 'super phenotypes' may be real, but they can only be 'super' under particular environmental conditions.

13.3 Dispersal syndromes within populations: dispersal reaction norms and syndromes in spiders

In spiders, aerial dispersal is mediated by distinct behaviours preceding transfer. By means of tiptoe behaviour (i.e. stretching of legs, raising abdomen, and producing silk threads) spiders initiate either long-distance dispersal when silk threads are transported in the air (ballooning) or short-distance dispersal when silk threads are used as bridges (rappelling) (Case Study II). Due to aerodynamic constraints, ballooning is restricted to smaller individuals. In temperate regions, these comprise predominantly the adults of smaller money spiders (Linyphiidae) or the juveniles of larger wolfspiders (Lycosidae). In the latter, routine cursorial movements (Bonte et al. 2004) or maternally assisted spreading of offspring (Bonte et al. 2007b) exist as alternative adult and natal dispersal mechanisms, respectively. Obviously, the different dispersal modes largely differ in efficiency and underlying costs. In case of ballooning, costs are directly related to the availability of suitable habitat within the dispersal perimeter (Englund and Hamback 2007),



Figure 13.1 Dispersal syndromes in *Melitaea cinxia*: (a) more mobile females reproduce at younger age, (b) females with a *Pgi* genotype that is related with high dispersal rate (*Pgi-f*) lay larger egg clutches, (c) females from newly established populations (open symbols), in which females have higher dispersal rate, lay eggs at faster rate, (d) and show a positive correlation between mobility and lifetime egg production, whereas females from old populations (closed symbols) show no such correlation. Data are adopted from Hanski *et al.* 2006 and Saastamoinen 2007a.

while short-distance dispersal success is more likely correlated with the spatial configuration of resources and habitat (Englund and Hamback 2007).

To investigate dispersal syndromes in spiders, we mainly applied a behavioural reaction norm approach (i.e. assessing the set of behavioural phenotypes that a single individual produces in a given set of environments; Dingemanse et al. 2010). We focused on species belonging to the genus Erigone which are predominantly associated with disturbed habitats. In these species, a strong female-biased dispersal is observed. In contrast to aerial dispersal in wolfspiders (Bonte et al. 2007a; Bonte et al. 2006), food shortage starvation induce a reduction of dispersal initiation in adult Erigone individuals (Bonte et al. 2008a). Dispersal was also strongly reduced by inbreeding (Bonte 2009) and the prevalence of endosymbiontic bacteria (Goodacre et al. 2009), suggesting a positive correlation between body condition and dispersal. This pattern has been confirmed in a study by varying body condition through variable developmental temperature (from 15-30 °C). When the different dispersal modes (so ballooning versus rappelling) were analysed separately, high developmental temperatures induced proportionally higher rates of rappelling relative to ballooning, while individuals raised at lowest temperatures dispersed more by ballooning compared to by rappelling (see Figures 13.2a,b). This shift in dispersal behaviour according to the developmental temperature is assumed to be adaptive since it reflects seasonal changes in habitat configuration related to the harvesting of crops (Bonte et al. 2008b). It thus suggests that temperature during development is perceived as a cue to adopt specific dispersal behaviours. Patterns were slightly different for males and females, with a positive correlation between the two dispersal modes among temperature treatments for females, and a slight negative one for males (Figure 13.2c). Interestingly, the positive correlations with proxies for body condition were also positive within temperature treatment (Bonte *et al.* 2008b).

Different temperatures during development subsequently induce different dispersal phenotypes. In females, these phenotypes are additionally linked to distinct settlement strategies. Lab experiments demonstrated that ballooning phenotypes of female spiders built webs above suitable microhabitat much faster than philopatric individuals (Figure 13.3a) and that they were much more eager to take over webs that were already occupied (Figure 13.3b; from Bonte et al. 2011). Long-distance dispersal phenotypes of the spider E. atra possess in consequence settlement advantages compared to residential phenotypes. This faster and more competitive settlement behaviour of ballooning compared to residential phenotypes can be the result of environmental constraints, enabling only those individuals in best conditions to emigrate. However, because ballooning dispersal has been shown to be a consistent trait and partly genetically determined (Bonte et al. 2009; Bonte and Lens 2007), they are likely to be adaptive dispersal strategies. Indeed, the evolution of positive covariation between individual condition and dispersal may evolve in landscapes with high levels of environmental stochasticity and either vacant or crowded habitat (Bonte and de la Pena 2009). These are the conditions experienced by Erigone spiders when emigrating in spring towards freshly sawn crops or emigrating en masse in autumn towards litter-rich vegetation, subsequently facing overcrowding due to concentration effects (Bonte et al. 2008b). The evolution of long-distance dispersal associated syndrome shows large parallels with the boldaggression-activity syndrome (a syndrome in which levels of aggression, boldness, and general activity are positively correlated; Sih et al. 2004; Chapter 10). Indeed, competitive behaviour during settlement



Temperature during development



Figure 13.2 Dispersal syndromes in *Erigone atra*: temperature during development induces different dispersal reaction norms for ballooning (a) and rappelling (b) propensity. When combining both, females show a positive correlation (full line) between long and short distance dispersal propensity (c - filled symbols), while males not (open symbols, dashed line). Error bars represent standard errors. Data are adapted from Bonte *et al.* 2008b.



Figure 13.3 Correlated responses of long-distance dispersal behaviour (ballooning) in *E. atra* females with web-building related behaviours: (a) latency to web building, and (b) web-take-over behaviour. From Bonte *et al.* (2011), used with permission from Elsevier.

implicates the presence of individual differences in boldness (i.e. taking decision to occupy new microhabitat sites) and aggression (i.e. the willingness to go into confrontation with conspecifics to take over web sites).

13.4 Context dependence of dispersal and the organization of syndromes

In spiders, dispersal strategies are strongly sexand context-dependent. Temperature during development (Bonte et al. 2008b), local densities of males and females (De Meester and Bonte 2010), but probably also internal physiological changes due to the presence of endosymbionts (Goodacre et al. 2009), provide information to which spiders adjust their dispersal behaviour. These contexts also induce differences in individual condition that impact (constrain) the eventual dispersal strategy and are likely to shape the direction of dispersal syndromes. The M. cinxia system additionally shows that dispersal syndromes can have a genetic background when dispersal or genetically correlated traits have a heritable background (example of Pgi-genotype affecting dispersal and fecundity via effects on flight metabolic rate). The strong selection for dispersal genotypes and associated syndromes as colonizers of vacant habitat in true metapopulations is then likely to scale up syndromes among populations (i.e. new versus old ones). The fact that dispersive individuals are not a random subsample from the (meta)population has profound consequences for population genetic structure and dynamics. In both E. atra and M. cinxia the positive relationship between body condition, dispersal, and settlement strategies can be expected to have a disproportionally larger effect on colonization potential and gene flow compared to species lacking this positive correlation. Of course, these conclusions are drawn from experiments under favourable conditions in which variation in body condition was prominent. Given the prominent importance of other proximate stress-inducing factors under natural conditions such as local density and the evolution of informed dispersal strategies (Chapter 10), it will be interesting to study reaction norms of these syndromes in relation to variable environmental contexts that impact dispersalrelated life-history traits (Reznick et al. 2000).

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