

Review

Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations

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Dispersal is one of the most fundamental components of ecology, and affects processes as diverse as population growth, metapopulation dynamics, gene flow and adaptation. Although the act of moving from one habitat to another entails major costs to the disperser, empirical and theoretical studies suggest that these costs can be reduced by having morphological, physiological or behavioural specializations for dispersal. A few recent studies on different systems showed that individuals exhibit personality-dependent dispersal, meaning that dispersal tendency is associated with boldness, sociability or aggressiveness. Indeed, in several species, dispersers not only develop behavioural differences at the onset of dispersal, but display these behavioural characteristics through their life cycle. While personality-dependent dispersal has been demonstrated in only a few species, we believe that it is a widespread phenomenon with important ecological consequences. Here, we review the evidence for behavioural differences between dispersers and residents, to what extent they constitute personalities. We also examine how a link between personality traits and dispersal behaviours can be produced and how personality-dependent dispersal affects the dynamics of metapopulations and biological invasions. Finally, we suggest future research directions for population biologists, behavioural ecologists and conservation biologists such as how the direction and the strength of the relationship between personality traits and dispersal vary with ecological contexts.

Keywords: dispersal; behavioural syndrome; colonization; invasion; metapopulation dynamics; G × E interactions

1. INTRODUCTION

Dispersal, the movement from a natal/breeding site to another breeding site, is one of the most fundamental life-history traits that affects processes as diverse as the dynamics and evolution of spatially structured populations, gene flow, species' distributions and species' ability to track favourable environmental conditions (Clobert *et al.* 2001, 2009; Bowler & Benton 2005). In the context of global change (climate change, habitat deterioration and fragmentation, biological invasion), dispersal behaviour is a crucial mechanism allowing species to respond to changing environmental conditions. Understanding the ultimate and proximate causes of dispersal is therefore crucial for population management and predicting consequences of environmental changes on species persistence and distributions.

Dispersal involves three successive behavioural stages: departure from the current patch, movement between patches (transience) and settlement in a new patch (Bowler & Benton 2005; Clobert *et al.* 2009). Several recent reviews have summarized factors driving dispersal decisions in these three distinct steps (Bowler & Benton 2005; Ronce 2007; Benard & McCauley 2008; Clobert *et al.* 2009), including intra-specific competition, predation risk, kin interaction, inbreeding risk, mate choice and habitat quality. Bowler & Benton (2005) and Clobert *et al.* (2009) stressed the fact that factors affecting decisions are likely to be different in the three stages of dispersal. For instance, kin competition is obviously more likely to affect departure from the natal site or, to a lesser extent, settlement in a novel site, rather than transience. A full assessment of the ecological and evolutionary consequences of dispersal thus requires an understanding of the mechanisms and rules governing the effects of these multiple factors at each behavioural stage of dispersal (Ronce 2007; Clobert *et al.* 2009). However, the three stages are rarely distinguished in empirical studies.

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Furthermore, the act of moving from one habitat to another entails major risks and costs to the disperser (Stamps 2001). Indeed, dispersal may be unsuccessful because the environment is too hostile, the surrounding areas may be unsuitable habitats and suitable habitat patches may be too distant. In addition, movement between habitats imposes opportunity costs in terms of time and energy usage. Settling into a novel habitat also entails costs associated with poor habitat choice (Edelaar *et al.* 2008) or a lack of familiarity with new congeners, predators or resource locations. Empirical and theoretical studies suggest that some of these costs can be reduced by having morphological, physiological or behavioural specializations for dispersal (Murren *et al.* 2001; Bowler & Benton 2005; Benard & McCauley 2008; Clobert *et al.* 2009).

In 1971, based on the idea that animal populations are a composite of qualitatively different individuals (Chitty 1960), Myers & Krebs (1971) published a large study on 'qualitative differences between dispersing and resident voles'. Recent years have seen a burst of renewed interest in this idea—that dispersing individuals are not a random subset of the population; instead, dispersers often differ from non-dispersers in phenotype (§2). The observed phenotypic differences may or may not involve consistent suites of traits (i.e. a dispersal syndrome), and can be caused by reversible or irreversible ontogenetic changes. In general, phenotypic differences between dispersers and residents are likely to exist, for example, if some morphological, physiological or behavioural specializations are needed to increase dispersal success. However, dispersal success is expected to depend on different factors in the three successive stages of dispersal. For instance, settlement success can depend on social integration abilities while transience success should depend more on locomotion/orientation abilities. We can thus expect that different phenotypic specializations help an individual to succeed in each of the three stages of dispersal. Moreover, since phenotypic traits differ in their ability to cope with various ecological contexts, phenotypic adaptations in dispersers are likely to depend upon the factors that motivate dispersal (Clobert *et al.* 2009). While many studies have looked at morphological specializations, variation in behavioural type and associated physiological traits can also be critically important.

In several taxa, comparisons between dispersers and residents have revealed differences in activity patterns, aggressiveness, social behaviour and mating decisions (§2). O'Riain *et al.* (1996) provide a classic example of phenotypic specializations of dispersers. In mole rats (*Heterocephalus glaber*), dispersers are larger and fatter than residents, but also have higher locomotor and feeding activities and a reduced participation in cooperative activities in the colonies they join (O'Riain *et al.* 1996). These phenotypic differences were quantified post-dispersal, but dispersers and residents seem to already behave differently before dispersal. This study and a few others strongly suggest the existence of disperser morphs with behavioural specializations maintained over their lifetime (§2).

Animal personality is one of the most exciting recent conceptual developments in animal behaviour

(aka temperament, behavioural type and behavioural syndrome; Dall *et al.* 2004; Sih *et al.* 2004; Bell 2006; Réale *et al.* 2007; Sih & Bell 2008). In many species, individuals exhibit relatively stable, consistent differences in behaviour across multiple contexts. While acknowledging individual variation is becoming commonplace, the link between personality traits and life-history strategies has been comparatively less studied (Réale *et al.* 2010), especially in spatial ecology. However, a few recent studies on different systems showed that individuals exhibit personality-dependent dispersal; e.g. where boldness, sociability or aggressiveness is associated with dispersal tendency (Fraser *et al.* 2001; Dingemanse *et al.* 2003; Cote & Clobert 2007; Duckworth & Badyaev 2007). While, to date, personality-dependent dispersal has been demonstrated in only a few species, we believe that it is a widespread phenomenon with important ecological consequences.

Here, we first review the evidence for behavioural differences between dispersers and residents and to what extent they constitute personalities. We focus, in particular, on interactions between personality and ecological context in driving variation in each of the three stages of the dispersal process: departure from a current patch, transience between patches and settlement in a new patch. In §2, we examine some potential proximate mechanisms that can both produce links between personality traits and dispersal behaviours, and allow these links to vary with the causes of dispersal. Although relationships between dispersal and personality traits appear complex, individual variation in various neurochemicals has been associated with variation in personality and with dispersal behaviour. Section 3 examines how personality-dependent dispersal affects population dynamics. In particular, we will focus on the dynamics of metapopulations and biological invasions. Finally, we suggest future research directions for population biologists, behavioural ecologists and conservation biologists interested in behavioural-type-dependent dispersal.

2. FROM BEHAVIOURAL-DEPENDENT TO PERSONALITY-DEPENDENT DISPERSAL

Phenotypic differences between dispersers and residents often involve morphological, behavioural or life-history traits that reduce the costs of dispersal and facilitate settlement (Clobert *et al.* 2009). The importance of behavioural traits in explaining individual strategies of dispersal has long been recognized for some taxa (e.g. mammals; Myers & Krebs 1971; Svendsen 1974; Bekoff 1977). An often unresolved issue is whether dispersing individuals differ in behaviour from residents across their lives or only when the decision to disperse is about to be made. While several studies showed that dispersers only became different from residents in behaviour in association with dispersal *per se* (table 1), other recent studies showed that dispersal tendencies are linked to individual differences in behavioural types or behavioural syndromes that can be stable over ontogeny or across situations. For example, dispersal propensity appears to be correlated with exploration/boldness, sociability or

Table 1. Behavioural differences between residents and dispersers. Here, we list examples of behaviour-dependent dispersal. In some studies, the behaviour involved in dispersal was consistent over time (i.e. personality-dependent dispersal). In other studies, behavioural differences between dispersers and residents were only temporary behavioural shifts inducing dispersal (usually before dispersal). Finally, in several studies, behaviours were observed only once (either before or after dispersal); in these studies, behavioural consistency still needs to be investigated. Residents are individuals from natal populations for 1–3, 5–13, 15, 16, 18–20 and individuals from the population where dispersers immigrated for 4, 5, 7, 14, 17. 1, Jokela *et al.* (2008); 2, Belthoff & Dufty (1998); 3, Bonte *et al.* (2004); 4, O’Riain *et al.* (1996); 5, Aragon *et al.* (2006b); 6, Krackow (2003); 7, Dingemanse *et al.* (2003); 8, Fraser *et al.* (2001); 9, de Fraipont *et al.* (2000); 10, Myers & Krebs (1971); 11, Duckworth & Badayev (2007); 12, Trefilov *et al.* (2000) and Mehlman *et al.* (1995); 13, Schradin & Lamprecht (2002); 14, Holekamp & Smale (1998); 15, Guerra & Pollack (2010); 16, Cote & Clobert (2007); 17, Abbot *et al.* (2001); 18, Cote *et al.* (2010); 19, Ims (1990); and 20, Blumstein *et al.* (2009).

behaviour	observed difference with residents	consistency of behaviour			time of measurement	
		consistent	temporary	not tested	pre-dispersal	post-dispersal
activity	dispersers are more active	1	2	3–5	1–3	4, 5
exploration/boldness	dispersers are faster explorer/bold	6–8		9	6–9	7
	dispersers are slower explorer/shy	10				10
aggressiveness	dispersers are more aggressive	11, 12		10	12	10–12
	dispersers are less aggressive			13–15	13, 15	14
sociability	dispersers are more social	1, 16			1, 16	16
	dispersers are less social	1, 5, 16–18		4, 19, 20	1, 16, 18, 20	4, 5, 16–19

aggressiveness before dispersal (Mehlman *et al.* 1995; Fraser *et al.* 2001; Dingemanse *et al.* 2003; Krackow 2003; Cote & Clobert 2007; Cote *et al.* 2010). Such behavioural differences between dispersers and residents may represent previously unrecognized ‘dispersal behavioural syndromes’ that can have important, novel implications for the dynamics of spatially structured populations (Duckworth 2008; Clobert *et al.* 2009). Here, we discuss each of three major behavioural axes (activity/boldness/exploration, sociability and aggressiveness) in the context of the three dispersal stages: departure, transience and settlement.

(a) Activity, exploration and boldness

Activity and exploration abilities might influence dispersing individuals at all stages of the dispersal process (table 1). For example, several studies suggest that dispersers and residents display consistent individual differences in activity/exploration. In mole rats, post-dispersal measurements show that dispersers have higher locomotor and feeding activities than non-dispersers (O’Riain *et al.* 1996). Similarly, Aragon *et al.* (2006a,b) and Meylan *et al.* (2009) showed that, in common lizards (*Lacerta vivipara*), dispersers were more active and display different foraging activity 8–10 months after the dispersal event. In male house mice (*Mus musculus musculus*), dispersal latency decreased with increasing exploratory activity measured before dispersal (Krackow 2003). While the consistency of exploratory activity was not tested in this study, dispersal latencies of fathers and sons were positively related and thus likely to be heritable in this species. Although heritability can change over a lifetime, given that repeatability often sets an upper bound for heritability (Dohm 2002), significant heritability should often translate to significant repeatability. Conversely, in two *Microtus* species, dispersing males showed less post-dispersal exploratory/activity

behaviour than resident males. Here, individual exploratory/activity behaviour was highly repeatable (Myers & Krebs 1971).

Consistent individual differences in exploratory behaviour have also been linked to behaviour during the transience and settlement stages. Two studies showed that activity in novel environments (referred to as exploration or boldness) is correlated to dispersal distance in the field (Fraser *et al.* 2001; Dingemanse *et al.* 2003). Fraser *et al.* (2001) showed that, in Trinidad killifish *Rivulus hartii*, dispersal distance in natural streams is positively related to individual score of exploration in unfamiliar habitat (aka boldness). Perhaps the most complete study demonstrating the link between behavioural syndromes and dispersal used great tits (*Parus major*) as a model system (Verbeek *et al.* 1994; Dingemanse *et al.* 2003; van Overveld & Matthysen 2009). First, they found consistent individual differences in exploratory behaviour. Artificial selection experiments over four generations produced fast exploring/bold versus slow exploring/shy individuals, thus demonstrating that exploratory behaviour and copying style are heritable (Dingemanse *et al.* 2003; van Oers *et al.* 2004). Most importantly, in the current context, Dingemanse *et al.* (2003) also showed that in nature, natal dispersal distance was correlated to exploratory behaviour and that immigrants were faster explorers than locally born individuals. These studies show that exploratory behaviour may affect both departure and transience/settlement decisions. Other studies, that do not mention personality, could also fit this pattern. For instance, in juvenile North American red squirrels (*Tamiasciurus hudsonicus*), the directionality exhibited during exploration as well as exploratory distance clearly predict the habitat where individuals settle (Haughland & Larsen 2004). This relationship was independent of natal habitat and could be explained by temporary as well as consistent individual differences in exploratory behaviour.

(b) Aggressiveness

A classic idea is that less aggressive, subordinate individuals are forced to disperse by aggression from more dominant individuals (Christian 1970; Bekoff 1977; Brandt 1992). For example, in house mice, young males have the greatest tendency to disperse, mainly because of aggressive interactions with dominant males (e.g. Pocock *et al.* 2005). Similarly, in a cichlid fish (*Neolamprologus multifasciatus*), the most aggressive females, females that had initiated more aggressive encounters in a dyad, had the largest subterritories, while less aggressive females with the smallest subterritories emigrated (Schradin & Lamprecht 2002). In addition, Guerra and Pollack recently showed that in a wing-dimorphic field cricket (*Gryllus texensis*), the longer winged (dispersive) individuals display lower levels of aggression (less likely to fight and attack) than their short-winged counterparts, which might constitute alternative reproductive strategies (Guerra & Pollack 2010).

In contrast, in other cases, more aggressive individuals tend to disperse more. For example, at peak population densities, *Microtus pennsylvanicus* males that dispersed are more aggressive than others (Myers & Krebs 1971). Similarly, in rhesus macaques (*Macaca mulatta*), aggressive individuals also tend to disperse earlier during their adolescence (Kaplan *et al.* 1995; Mehlman *et al.* 1995; Trefilov *et al.* 2000). Mehlman *et al.* (1995) showed that the concentration in cerebrospinal fluid (CSF) of the serotonin metabolite 5-hydroxyindoleacetic acid (5-HIAA), which is consistent over time (Howell *et al.* 2007), is negatively correlated to aggressiveness in the natal group and positively correlated with age at emigration from the natal group (see also §3). Thus, aggressive individuals disperse earlier than less aggressive ones prior to or during adolescence (note that this relationship is reversed for individuals that dispersed after the age of sexual maturity; Howell *et al.* 2007).

In some species such as the mongoose (*Mungos mungo*), two distinct modes of dispersal exist (Cant *et al.* 2001). Subordinates can be aggressively driven out of the pack by dominant individuals, or groups of individuals can emigrate voluntarily to form new packs and fight much more than resident packs to establish their home range. This makes it harder to predict whether the more aggressive or the less aggressive individuals should be more prone to disperse (Bekoff 1977; Brandt 1992). This discrepancy is likely to be due to interactions with habitat quality and the population age or sex structure.

While we previously showed that aggressiveness may affect the departure from their population, aggressiveness is also involved in the immigration/settlement process (Brandt 1992). Indeed, settlement success can be enhanced by having dispersal specializations such as submissive behaviours or secretive strategies. This is well known in mammals where aggression by residents towards potential immigrants limits movement into groups (lion tamarins, Baker & Dietz 1996; gorilla, Watts 1994), but it has also been shown in other taxa (e.g. Siberian jay, Griesser *et al.* 2008; common lizards, Aragon *et al.* 2006a). Higher

aggressiveness towards immigrants can be explained by the fact that immigrants are often intruders in resident territories, and individuals are usually more aggressive to unrelated individuals than to their kin or to familiar individuals (i.e. Dear Enemy Hypothesis: Fisher 1954). Aggression by residents can be a significant source of wounds and mortality (e.g. Smith & Batzli 2006), and thus a major cost at dispersal. Alternatively, higher aggressiveness might enhance an individual's success at integrating into a new population. This prediction is supported by studies on western bluebirds (Duckworth & Badyaev 2007; Duckworth 2008, 2009; Duckworth & Kruuk 2009). At the interspecific level, Duckworth & Badyaev (2007) showed that because dispersing western bluebird individuals were also highly aggressive after immigration, this allowed this species to displace and ultimately exclude an interspecific competitor, the mountain bluebird, from invaded sites. Aggressive behaviour in western bluebirds was heritable, repeatable and consistent within individuals, independent of local competitor density. These results indicate the existence of an aggressive personality trait and suggest a strong role of personality in dispersal success and range expansion. In addition, in rhesus macaque males, social dominance rank in the new troop (after they emigrated to a new troop) was negatively correlated with juvenile CSF 5-HIAA concentrations, even if it has been shown that, males with low CSF 5-HIAA concentrations are less likely to be sought out as sexual partners by receptive females following emigration than are males with high CSF 5-HIAA concentrations (Howell *et al.* 2007).

More generally, it is worth noting that many studies relating dispersal and aggressive behaviour did not measure individual aggressiveness under standardized conditions, but instead examined aggression or dominance in observed aggressive encounters in uncontrolled conditions. Under natural or semi-natural conditions, variation across focal animals in rates and levels of aggressive behaviour is affected by a variety of factors besides their own aggressiveness, e.g. variation across individuals in local population density or encounter rates with conspecifics, variation in the extent to which conspecifics instigate aggressive interactions with the focal animal and variation among focal animals in the type of individuals they encounter on an ongoing basis. Studies controlling for these factors are, however, rare. For example, among the cited studies, aggressiveness has been measured in a standardized situation for *M. pennsylvanicus* (Myers & Krebs 1971) but not for rhesus macaques (*M. mulatta*; Mehlman *et al.* 1995), the mongoose *M. mungo* (Cant *et al.* 2001), the cichlid *N. multifasciatus* (Schradin & Lamprecht 2002, table 1) or the male spotted hyaenas (*Crocuta crocuta*, Holekamp & Smale 1998, table 1). An example of the measurement of aggressiveness in a natural but standardized situation is the work on mountain and western bluebirds, where aggressiveness was measured by experimentally simulating a territorial intrusion of a common interspecific competitor. Finally, in the rhesus macaques, it is worth noting that aggressiveness was related to the concentration of serotonin metabolite as well as to the polymorphism

in the promoter region of the serotonin transporter (Krawczak *et al.* 2005). Therefore, their measurements of aggressive behaviours probably reflect intrinsic individual aggressiveness. In general, aggressive behaviour should be more often measured in a standardized situation to clearly understand the link between individual variation in aggressiveness and dispersal behaviour.

(c) Sociability

Recent theoretical and empirical work on the evolution of altruism, sociality and dispersal suggests links between dispersal and sociality (Ims 1990; Sinervo & Clobert 2003; Le Galliard *et al.* 2005; Schtickzelle *et al.* 2009). However, individual variation in social behaviour (i.e. sociability) has only rarely been related to dispersal behaviour. This is surprising since the social cohesion hypothesis was developed more than 30 years ago (Bekoff 1977). In his review about mammal dispersal, Bekoff (1977) predicted that individuals who socialized with or are not repulsed by others were less likely to disperse. A recent study corroborated this hypothesis, showing that female yellow-bellied marmots (*Marmota flaviventris*) that had affiliative interactions with more individuals, and those that were more socially embedded in their groups, were less likely to disperse afterwards (Blumstein *et al.* 2009). If an individual's low social embeddedness reflects its tendency to avoid conspecifics (as opposed to conspecifics' avoiding the individual), then these findings might reflect individual variation in the tendency/ability to socialize, a personality trait named sociability. Indeed, Svendsen (1974) showed that social female yellow-bellied marmots were clumped in harems while asocial females were living in peripheral burrows at colonies or in satellite sites.

A few studies have more explicitly examined the potential correlation between sociability and dispersal. Ims (1990) suggested that individual decisions whether to disperse or not in female grey-sided voles (*Myodes rufocanus*) depended on behavioural characteristics, and found dispersal distance to increase with social avoidance behaviour measured after dispersal. Similarly, O'Riain *et al.* (1996) showed that dispersers participate less in cooperative maintenance tasks of the colony they have integrated into. These studies do not, however, put their results in the context of personality traits. Social personality trait, or sociability, has been linked with dispersal strategies in the common lizard (Cote & Clobert 2007) and in humans (Jokela *et al.* 2008). In the common lizard, dispersal behaviour depends on the relationship between individual sociability measured a few days after birth and local population density. Asocial individuals, who have increased fitness at low density and prefer to stay away from conspecifics, tend to disperse when densities get too high, while social individuals, who actively seek out conspecifics and have increased fitness at high densities, disperse when densities are too low (Cote & Clobert 2007; Cote *et al.* 2008). These results fit previous findings on the same species, showing that, 8 months after dispersal, dispersers still try to escape groups of interactive individuals (Aragon *et al.* 2006b; Meylan

et al. 2009). Interestingly, these results are independent of morphological characteristics that predict competitive abilities in this species.

The pattern of social type interacting with density to produce dispersal patterns is manifest among humans as well. Among Finnish people, individuals with higher sociability scores at the beginning of the study were more likely to migrate into cities afterward, while lower sociability individuals were more likely to migrate out of cities (Jokela *et al.* 2008). Finally, we recently showed that sociability is an important indicator of dispersal distance in the invasive mosquitofish (*Gambusia affinis*), suggesting personality-biased dispersal at an invasion front (Cote *et al.* 2010, see §3).

Sociability-dependent dispersal should be distinguished from aggressiveness-dependent dispersal. Because more aggressive animals tend to be less sociable, it can be difficult to tease apart the effects of these two behavioural tendencies on dispersal. For example, Gerlach's (1998) test of the 'social cohesion hypothesis' on feral house mice (*Mus musculus domesticus*) found that male emigrants were less integrated in cohorts of male littermates, suggesting that social ties matter for dispersal behaviour. However, male emigration was actually caused by aggression of the dominant male in competition for the top rank within the group; cohorts of littermates protected socially integrated, single males from attacks by the dominant male (Gerlach 1998). In contrast, Blumstein *et al.* (2009) showed that dispersal behaviour in yellow-bellied marmots can be largely predicted by affiliative interactions, but does not depend on the rate of agonistic behaviour.

(d) Personality-dependent dispersal in varying ecological contexts

Finally, the direction and the strength of the relationship between personality traits and dispersal behaviour should also depend on ecological and social contexts (Cote & Clobert 2007; Clobert *et al.* 2009; van Overveld & Matthysen 2009). Given that personality types differ in their abilities to cope with various ecological factors (e.g. with high density, kin and non-kin competition or predation; Dingemanse & Réale 2005; Smith & Blumstein 2008), individuals of different personalities should react differently to various ecological and social contexts and their dispersal tendencies should depend in predictable ways on the interaction between personality type and ecological conditions. For instance, sociability-dependent dispersal should vary with population density (Cote & Clobert 2007). Since asocial and social individuals differ in their attraction towards and tolerance of conspecifics, they should display different reactions to varying population density. In a low-density population, social individuals might be more likely to disperse to search for more dense populations (and thus more conspecifics), while asocial individuals should disperse more from high-density populations where conditions are too crowded relative to their low social tolerance.

Similarly, boldness-dependent dispersal may depend on predation risk. Interestingly, predation

risk could cause either bolder or shier individuals to disperse more. If shy individuals generally tend to avoid risk, they might disperse to avoid predators. On the other hand, if bold individuals suffer higher predator-induced mortality rates than shy individuals (Smith & Blumstein 2008), then bolder individuals should be particularly likely to disperse to avoid predators. How personality-dependent dispersal patterns vary with ecological and social contexts has rarely been studied (Cote & Clobert 2007) and is thus one crucial future research direction. In particular, context dependency in personality-type-dependent dispersal can create important heterogeneity in dispersal syndromes that can have important effects on the dynamics of spatially structured populations (Clobert *et al.* 2009).

3. PROXIMATE FACTORS ASSOCIATED WITH PERSONALITY-DEPENDENT DISPERSAL

Individual variation in various neurochemicals (e.g. stress hormones, other steroid hormones, serotonin and dopamine) has been associated with variation in both personality traits and dispersal behaviour (see below). Although several physiological mechanisms plausibly underlie the joint development of dispersal behaviour and personality traits, few studies have examined factors leading to the correlation between personality and dispersal behaviour (Trefilov *et al.* 2000; Duckworth 2009; Duckworth & Kruuk 2009). In this section, we discuss proximate pathways connecting dispersal behaviour and personality traits.

Recent papers suggest that variation in personalities might be associated with, and ultimately explained by, individual differences in morphology, physiology and/or neuroendocrine responses. For instance, extant studies of individual variation in personality traits have often focused on the hormonal stress response where variation in corticosterone levels (basal and induced) is associated with variation in several personality axes such as boldness, neophobia, exploration, risk-taking behaviour and proactive–reactive strategies (Koolhaas *et al.* 1999; de Fraipont *et al.* 2000; Carere *et al.* 2003; Martins *et al.* 2007; Spencer & Verhulst 2007). Corticosterone has also been shown to redirect behaviour towards dispersal by influencing body condition, locomotion and foraging behaviour (Silverin 1997; Belthoff & Dufty 1998; de Fraipont *et al.* 2000; Dufty & Belthoff 2001). Furthermore, maternal stress hormones have been shown to influence offspring behaviour and, in particular, the dispersal propensity of the offspring (de Fraipont *et al.* 2000; Meylan *et al.* 2002; Meylan & Clobert 2005). Therefore, glucocorticoids, though maternal effects, can modify both offspring behavioural profile (aggressiveness, activity, social tendency) and dispersal propensity and are thus a potential proximate link between personality and dispersal behaviour.

Other hormones could also have similar effects. Maternal testosterone level is known to influence offspring behavioural traits like aggressiveness or risk-taking behaviour (Groothuis & Carere 2005) as well as dispersal propensity (Dufty & Belthoff 2001). For example, perinatal exposure to testosterone

subsequently results in dispersal of treated individuals in Belding's ground squirrels (Holekamp *et al.* 1984; Nunes *et al.* 1998). These results support the organizational hypothesis in which gonadal steroids act during foetal or neonatal life on neural tissues destined to mediate behaviours. Holekamp *et al.* (1984) further suggested that testosterone may promote dispersal behaviour through its mediating effects on juveniles' exploratory and social behaviours, and on their responsiveness to frightening stimuli.

Because maternal hormones vary with both the personality of the mother and her environment (that might also be the offspring's future environment), maternal effects are a good candidate for mediating the context-dependency of personality–dispersal correlation. For example, in great tits, fast/bold individuals display a lower increase in corticosteroid level after a social stress than slow/shy ones (Carere *et al.* 2003). If maternal effects have a genetic basis, then this indirect genetic effect can thus shape offspring phenotype (e.g. personality and dispersal behaviour) to adapt to the natal environmental conditions or to induce movement out of the natal area. Postnatal environment will ultimately interact with offspring phenotype to engage individuals in the right dispersal decisions. Such mechanisms can explain why some personality traits can be either positively or negatively related to dispersal behaviour depending on environmental conditions.

Variations in neuroendocrine levels can depend on genes (G), environmental experiences (E) and the G × E interaction (Dufty *et al.* 2002; Groothuis & Carere 2005; van Oers *et al.* 2005; Stamps & Groothuis 2010a). In turn, these can influence personality-dependent dispersal in two ways (figure 1). First, the coordinated expression of traits (dispersal behaviour and personalities) could be due to shared dependence of traits on genetic and environmental factors during ontogeny (Duckworth & Kruuk 2009). The internal state of an individual may then determine both its dispersal inclination and behavioural profile (Holekamp 1986; Belthoff & Dufty 1998). The suggestion is that the correlation between personality and dispersal *inclination* is coordinated by a shared G × E interaction but the actual dispersal decision that any given individual takes is influenced by its postnatal environment (figure 1a).

For example, Duckworth & Kruuk (2009) showed that aggression and dispersal are phenotypically and genetically correlated in the western bluebird. They concluded that common developmental mechanisms influence both dispersal propensity and consistent aggressiveness within individuals (Duckworth & Kruuk 2009). While the integration between aggressiveness and dispersal is coordinated by shared genes, the actual strategy that emerges also depends on environmental variation (Duckworth 2009; Duckworth & Kruuk 2009). The correlation between dispersal and aggressiveness is favoured because aggressive individuals have higher settlement success after dispersing. This should favour pleiotropy or epistasis among genes that control for behavioural traits through, for example, the coexpression of genes that affect the development of diverse neurophysiological pathways (Sinervo *et al.* 2008).

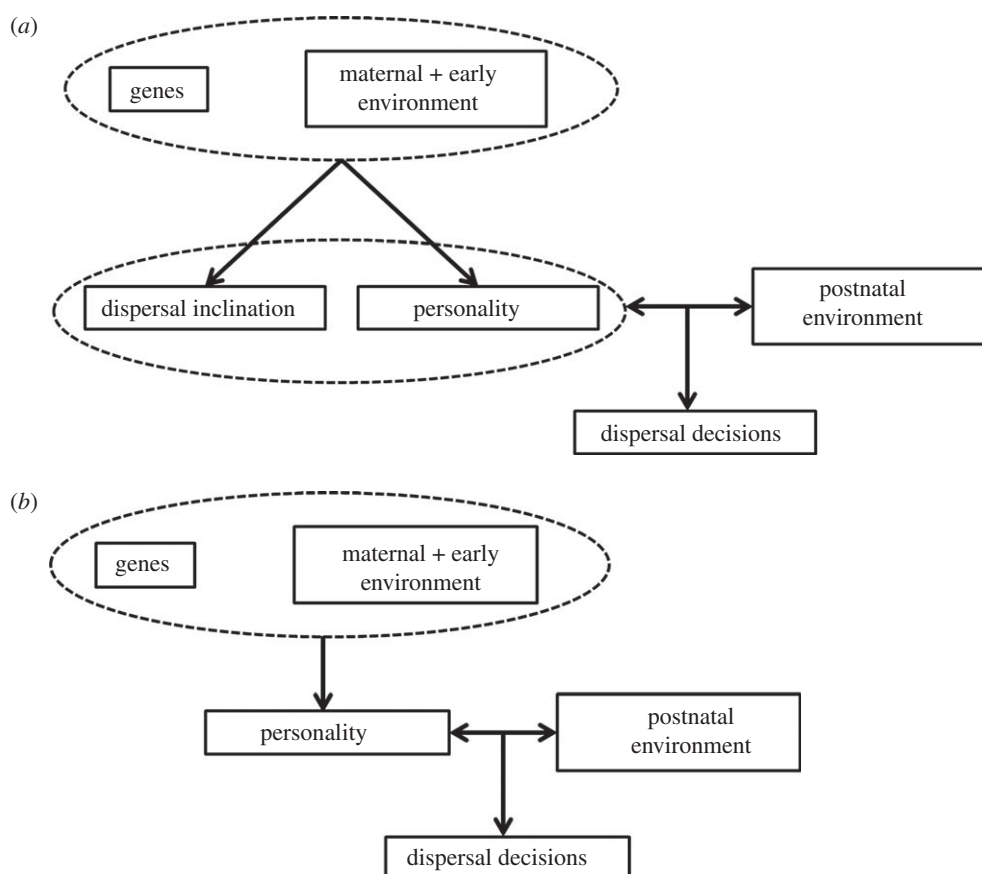


Figure 1. Two suggested ontogenetic pathways linking dispersal behaviour and personality traits in varying environmental conditions. (a) The correlation between personality and dispersal *inclination* is coordinated by a shared $G \times E$ interaction, but the actual dispersal decisions that any given individual takes are influenced by its postnatal environment. (b) The set of personality traits is determined by $G \times E$ interactions during offspring development, and then dispersal decisions depend on the interaction between environmental conditions and personality traits.

A second scenario suggests a hierarchy of effects (figure 1b). The behavioural profile (set of personality traits) is determined by $G \times E$ interactions during offspring development (Stamps & Groothuis 2010a,b). The behavioural profile affects individual performance/reaction to different environmental conditions. For example, individual variation in sociability affects individual performance in populations of varying densities (Cote & Clobert 2007), and individual variation in the boldness axis affects performance in the absence/presence of predators (Bell & Sih 2007; Stamps 2007). Adaptive dispersal decisions should thus depend on the interaction between environmental conditions and personality (Meylan *et al.* 2009). This scenario is the proposed mechanism for personality-dependent dispersal in rhesus macaques (Trefilov *et al.* 2000). In this species, only males emigrate, while females remain in their natal groups throughout their lives. Most but not all male rhesus macaques leave their natal group, but the age at which males disperse from their natal groups is highly variable. In young rhesus macaques, CSF 5-HIAA concentration was positively correlated with age at emigration from the natal group. The total time spent in close proximity to other group members was positively correlated to CSF 5-HIAA concentration because individuals with low concentrations exhibit more violent behaviour. Trefilov *et al.* (2000) suggested that impulsive behaviour together

with a higher tendency towards risk-taking activities might drive early dispersal of aggressive young male rhesus macaques. Furthermore, Krawczak *et al.* (2005) showed that a polymorphism in the promoter region of the serotonin transporter creates differences in age-dependent reproductive success, which in turn is likely to affect age at natal dispersal (Trefilov *et al.* 2000; Krawczak *et al.* 2005).

Similarly, even if indirectly suggested, the personality-dependent dispersal observed in great tits matches this second scenario (Dingemanse *et al.* 2003; Fidler *et al.* 2007). Fidler *et al.* (2007) suggested that polymorphisms in the dopamine receptor *DrD4* gene are associated with variation in the level of exploratory/novelty-seeking behaviour in this species (but see Korsten *et al.* 2010). High levels of exploratory/novelty-seeking behaviour should lead to subsequent differences in dispersal behaviour. In this scenario, the actual dispersal decision is not directly under the control of shared developmental processes with personality traits. Instead, variation in the dispersal decision is an emergent consequence of individuals expressing personality traits in specific environmental conditions. Even if the connection is indirect, if the coexpression of personality and dispersal is positively selected (e.g. aggressive macaques will probably die if they do not disperse), then pleiotropy between these traits should be favoured over the long term.

4. CONSEQUENCES OF PERSONALITY-DEPENDENT DISPERSAL FOR SPATIALLY STRUCTURED POPULATIONS

For several decades, behavioural ecologists have emphasized the importance of taking into account individual behaviour to understand population dynamics, species interactions, coexistence and extinction (MacArthur 1972; Sih 1987; Sutherland 1996; Courchamp *et al.* 2008). Interestingly, while dispersal is clearly a key to understanding metapopulation dynamics and evolution (Hanski & Gaggiotti 2004), until recently, few studies have looked at how individual differences in dispersal behaviour might have important effects on colonization, range expansion and more generally on the balance between extinction and recolonization.

When dispersal depends on both the individual's personality and the ecological context, the phenotypic composition of the pool of dispersers (both their average personality and the heterogeneous mix of personalities) can vary in complex ways, which, in turn, can have important effects on the dynamics of spatially structured populations (Clobert *et al.* 2009). A good example of how the average personality of dispersers influences spatial population dynamics comes from studies on western bluebirds where colonists to new sites tend to be aggressive individuals (Duckworth & Badyaev 2007). The coupling of dispersal and aggression has led to a wave of range expansion, with highly aggressive types dispersing to the front of range expansion and displacing a competitor, the mountain bluebird (Duckworth & Badyaev 2007; Duckworth 2008).

The possibility that a mix of behavioural types may facilitate rapid invasions comes from the observation that different behavioural traits may be necessary to successfully complete different stages of the invasion process. For example, the traits required to spread through an environment quickly might be incompatible with those required to settle in already existing populations or to deal with high- versus low-competition environments. Specifically, individual differences in sociability may lead to biased dispersal of different types among populations of different densities. Asocial individuals are likely to stay in low-density patches and leave only when populations become dense, while social individuals are not likely to colonize empty sites, but are more likely to tolerate high densities (Cote & Clobert 2007; Cote *et al.* 2010; J. Cote *et al.* 2010, unpublished data on *Gambusia*). Populations with a mix of personality types (e.g. asocial and social individuals) can thus speed up the spread of an invasion (figure 2). This scenario is also one explanation for the observed differences in the phenotypic composition of recently colonized populations compared with older populations for traits linked with dispersal (Duckworth & Badyaev 2007).

Heterogeneity in the dispersers' personality traits can also affect the dynamics of metapopulations. Classical metapopulation systems represent an extreme form of patchiness, and their dynamics depend on local extinction, colonization owing to dispersal into locally extinct patches and reinforcement owing to dispersal into extant patches (Hanski & Gaggiotti 2004).

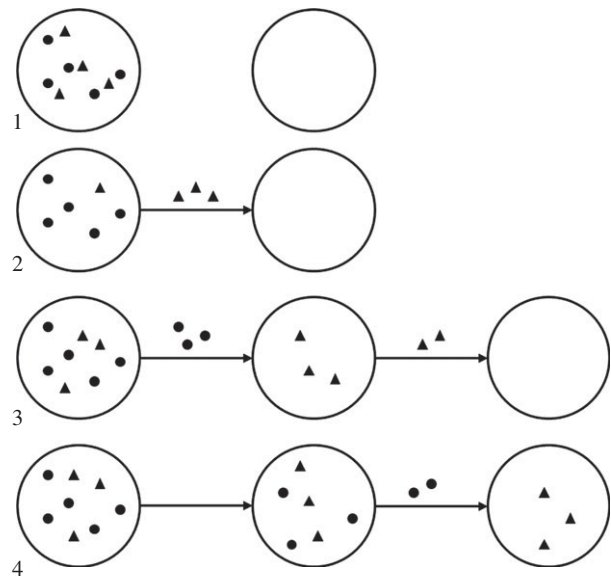


Figure 2. Hypothetical scenario about the consequences of personality-dependent dispersal on biological invasions. In this scenario, colonizers are individuals with a specific behavioural syndrome that first establish new populations, and these newly colonized populations are then reinforced by joiners, individuals with a different behavioural syndrome from the colonizers. Filled triangles, behavioural syndrome A (e.g. bold, fast explorer, aggressive and/or asocial); filled circles, behavioural syndrome B (e.g. shy, slow explorer and/or social).

Colonization and reinforcement might not necessarily involve individuals with similar personality traits, and thus the variability in dispersers' personality traits may facilitate both the recolonization of extinct patches and the reinforcement and rescue of already existing patches in a metapopulation (Clobert *et al.* 2004). The heterogeneity in behavioural-type-dependent dispersal can either stabilize the system and create an equilibrium through spatio-temporal variation in the kind of individuals dispersing, or destabilize it whenever the dominant dispersal cause is producing personality types that are not appropriate to the current environmental conditions (Clobert *et al.* 2009).

5. CONCLUDING REMARKS AND FUTURE DIRECTIONS

Dispersal is a fundamental component of both ecology and evolution, and affects processes as diverse as population growth, metapopulation dynamics, gene flow and adaptation. Dispersal is critical not only for basic ecology, but also for applied issues, including management of declining, threatened or endangered species in fragmented habitats and, on the opposite end of the spectrum, management of invasive species (or species expanding their ranges). Dispersers are different from non-dispersing individuals for a suite of phenotypic traits, including their behavioural profile. Some decades ago, Myers & Krebs (1971) were already testing the idea that dispersers are not a random subset of the population and that they differ qualitatively from residents. However, recent

work has stimulated a renewed interest in research on the relationship between behaviour and dispersal (Bowler & Benton 2005; Benard & McCauley 2008; Clobert *et al.* 2009).

One new insight is that phenotypic differences between dispersers and residents are not temporary phenotypic changes, but remain consistent though their life cycle. Although Bekoff (1977) suggested accounting for individual variation in behaviour decades ago, the existence of personality traits has rarely been mentioned in spatial ecology and even less in metacommunity ecology. Future work should investigate whether the specific behavioural profile of dispersers is a temporary shift or a more consistent behavioural syndrome. In this context, it can be crucial to distinguish situations where individuals differ in a personality trait, which then predicts their dispersal latency/distance/success, from situations where, after having dispersed, individuals exhibit different behaviours compared with natal non-dispersers. In the latter situation, behavioural differences might be consequences rather than causes of dispersal. For example, after dispersal, a disperser might differ behaviourally because it is unfamiliar with the local conditions or because these behavioural differences are the best strategy to integrate into a new population. However, several studies reported that disperser behavioural differences are consistent over long periods of time. For example, the consistency of behaviour has been observed up to a year after dispersal events in common lizards (Aragon *et al.* 2006b; Cote & Clobert 2007; Meylan *et al.* 2009), and up to five months in mosquitofish (Cote *et al.* submitted), and levels of serotonin metabolite as juveniles are correlated to both levels of serotonin metabolite and aggressiveness 8–10 years later in the rhesus macaque (Howell *et al.* 2007). This suggests that, at least in some species, the disperser behavioural syndrome is not simply a short-term shift in behaviour in response to conditions associated with dispersal *per se*, or establishment in a new site.

Recent studies suggest that not only do dispersers have particular phenotypic traits, but that this dispersal phenotypic syndrome should vary with ecological and social contexts. In other words, the interaction between the ecological context and the phenotype drives individual variation in dispersal decisions. How the personality of dispersers varies with the cause of dispersal is mostly unknown (but see Cote & Clobert 2007). This question should become an important research objective in dispersal studies. Finally, as illustrated by the intensive work on western bluebirds (Duckworth's papers), personality-dependent dispersal can have major consequences on the dynamics of spatially structured populations. Accounting for personality traits should provide stimulating advances for empirical and theoretical studies on metapopulation dynamics, biological invasion, range expansion as well as for conservation and wildlife management. For instance, personality-dependent dispersal might play a key role in re-introduction strategies. To be successful, re-introduced individuals must have particular characteristics such as a high probability to stay on the release site, an ability to

perform at low density, etc. Indeed, upon arrival in a novel environment, an individual can either stay in the release site or reject it and leave. Individual reaction to novelty can thus affect the probability that introduced individuals reject the novel habitat as well as their reaction to human activities (Pinter-Wollman 2009). By using appropriate behavioural tests, individuals with the right personality-dependent dispersal profile can be selected and released. However, releasing only individuals with specific personality traits, and thus with a restricted diversity compared with natural populations, might also have complex negative consequences for the persistence and the dynamics of those novel populations.

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