IDEA AND PERSPECTIVE

Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations

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Abstract

There is accumulating evidence that individuals leave their natal area and select a breeding habitat non-randomly by relying upon information about their natal and future breeding environments. This variation in dispersal is not only based on external information (condition dependence) but also depends upon the internal state of individuals (phenotype dependence). As a consequence, not all dispersers are of the same quality or search for the same habitats. In addition, the individual's state is characterized by morphological, physiological or behavioural attributes that might themselves serve as a cue altering the habitat choice of conspecifics. These combined effects of internal and external information have the potential to generate complex movement patterns and could influence population dynamics and colonization processes. Here, we highlight three particular processes that link condition-dependent dispersal, phenotype-dependent dispersal and habitat choice strategies: (1) the relationship between the cause of departure and the dispersers' phenotype; (2) the relationship between the cause of departure and the settlement behaviour and (3) the concept of informed dispersal, where individuals gather and transfer information before and during their movements through the landscape. We review the empirical evidence for these processes with a special emphasis on vertebrate and arthropod model systems, and present case studies that have quantified the impacts of these processes on spatially structured population dynamics. We also discuss recent literature providing strong evidence that individual variation in dispersal has an important impact on both reinforcement and colonization success and therefore must be taken into account when predicting ecological responses to global warming and habitat fragmentation.

Keywords

Colonization, dispersal, information, invasion, plasticity, syndrome.

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INTRODUCTION

Most organisms have the capacity to disperse from one place to another at some spatial scales and during some life stages. *Dispersal* (see the Glossary for a definition of italicized terms) may allow the exploitation of spatially and temporally variable resources, and is essential for most species to persist in their ever changing natural environment (Ronce 2007). Unsurprisingly, the importance of dispersal behaviour for the ecology and genetics of wild populations is becoming increasingly apparent as more populations face the major threats posed by global climate change and the fragmentation of their habitat. For example, the ability of species to respond to climate warming depends upon their potential for colonizing new habitats and adapting to changed conditions. This is well illustrated by the ecological and evolutionary consequences of climate warming at the margins of the ranges of some butterflies and crickets (e.g. Thomas *et al.* 1998; Hill *et al.* 1999).

Previous attempts to model spatial population dynamics and species distribution have relied on the assumption that

individuals move randomly in a heterogeneous landscape (reviewed in Patterson *et al.* 2008). Conversely, when behavioural ecologists study animal dispersal or *habitat selection*, they usually assume that individuals move for particular reasons and select their new place to live non-randomly (Clobert *et al.* 2001). Evolutionary models and empirical studies aiming to understand why animals disperse provide overwhelming evidence that several factors influence the costs and benefits of dispersal at the three distinct stages of departure, transience and settlement (Clobert *et al.* 2004; Bowler & Benton 2005). Such factors include intraspecific competition, kin competition, mate choice and habitat quality. A proper 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 *et al.* 2001).

A recurrent finding of evolutionary models of dispersal (Bowler & Benton 2005) is that the balance between the costs and benefits of dispersal depends on the factor driving the evolution of this behaviour, but also on the internal state of the individual (e.g. body condition, sex). As a consequence, not only may individuals leave their populations for different reasons, but dispersers are also found to differ from residents in a suite of phenotypic traits, sometimes in a striking manner (e.g. O'Riain *et al.* 1996; Zera & Denno 1997). The study of habitat selection has also highlighted that multiple criteria affect settlement decisions and that these criteria differ among individuals (Stamps 2001). Thus, in animals, individual decisions to leave a patch and settle in a new one are often both *condition-dependent*, which means that individuals rely on a set of external cues to adjust their dispersal tactics (e.g. Denno & Roderick 1992; Matthysen 2005), and *phenotype-dependent*, which means than dispersal propensity correlates with a suite of phenotypic traits (Fig. 1).

Until recently, the mechanisms linking condition-dependence during departure, transience and settlement stages and phenotype-dependent dispersal remained relatively unexplored. The current review highlights three important processes that link condition-dependent dispersal, phenotype-dependent dispersal and habitat choice in wild animals: (1) the relationship between the cause of departure and phenotype-dependent dispersal; (2) the relationship between the cause of departure and settlement behaviour and (3) the concept of *informed dispersal*, where individuals gather and transfer information before and during their movements through the landscape (Fig. 1). We discuss the ecological implications of these processes and propose most fruitful avenues for future research on dispersal behaviour.
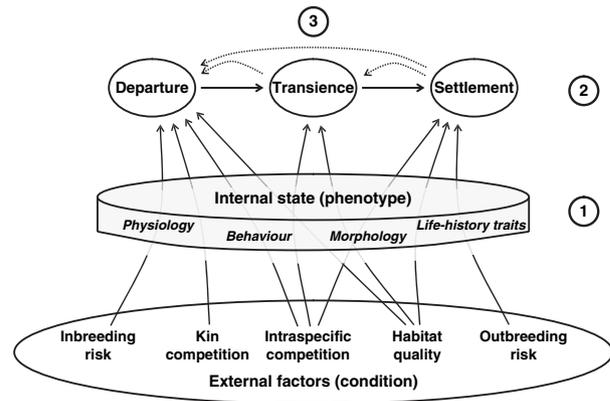
Figure 1 A conceptual framework to investigate individual variation in dispersal. Relationships between the three dispersal stages (departure, transience and settlement), phenotype-dependent dispersal (i.e. dependence on internal state) and condition-dependent dispersal (i.e. dependence on external factors) are illustrated. We discuss here three main processes shaping individual variation in dispersal: first, phenotypic differences between residents and dispersers should depend on external factors that cause dispersal (1); second, individuals may vary in their sensitivity to conditions encountered during transience and at settlement, given their phenotype and dispersal motivation (2); and third, a transfer of information through individual movements across the landscape might cause unexpected feedbacks between dispersal stages (3, dotted arrows).

HYPOTHESES AND MECHANISMS LINKING PHENOTYPE- AND CONDITION-DEPENDENT DISPERSAL

Phenotypic differences between dispersers and non-dispersers (hereafter named residents) have been described in almost all taxonomic groups investigated so far, from unicellular organisms to insects and mammals (Swingland 1983; Bowler & Benton 2005). These phenotypic differences have been found for a variety of physiological, morphological, behavioural and life-history traits. 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 ontogenic changes (Table 1). In general, phenotypic differences between dispersers and residents are likely to exist for three main reasons: (1) if some morphological, physiological or behavioural specializations are needed to increase dispersal success; (2) if energetic investment in dispersal is substantial and must trade off with energetic allocation to other traits and (3) if some traits not needed for a high dispersal capacity *per se* benefit dispersers more than residents. An example of the first scenario is the combination of an active metabolism, strong wing muscles and an appropriate body shape in insects that rely on wings to disperse long distances (Zera &

Table 1 Phenotypic differences between residents and dispersers have been observed in many species

	Phenotypic traits	Observed difference with residents	Genetic basis	References
Physiology	Juvenile hormone	Differences in circadian patterns	Yes	(1)
	Testosterone levels	Immigrants have higher T levels	No	(2, 3)
	Corticosterone levels	Dispersers have higher CORT levels	No	(4, 5)
	Serotonin activity	Dispersers have higher serotonin activity	Yes	(6)
Behaviour	Exploration	Dispersers are faster-exploring	Some	(5, 7, 8)
		Dispersers are slower-exploring	No	(9)
	Sociality	Dispersers are more social	No	(10)
		Dispersers are less social	Some	(10–12)
	Aggressiveness	Dispersers are more aggressive	Some	(9, 13)
		Dispersers are less aggressive	No	(14)
Morphology	Body size	Dispersers are larger	Some	(14–19)
		Dispersers are smaller	No	(16)
	Body condition	Dispersers are fatter	Some	(5, 14, 20, 21)
Life history	Fecundity	Dispersers have larger fecundity	Some	(22–24)
	Survival	Dispersers have lower survival	Yes	(24)

Here, we list examples of phenotype-dependent dispersal (some being genetically based) from disparate studies. In some species (e.g. reference 8), several traits have been found to be related and to form dispersal syndromes. Reverse trends have been found both among (e.g. references 9 and 14) and within the same species (e.g. reference 10). Plants have not been included, but dispersal is also associated with morphological and life-history specializations in plants (e.g. Imbert & Ronce 2001).

1. A. J. Zera, Z. Zhao, K. Kaliseck, *Physiol. Biochem. Zool.* **80**, 592 (2007); 2. K. E. Holekamp, C. L. Sisk, *Horm. Behav.* **44**, 385 (2003); 3. R. Woodroffe, D. W. MacDonald, J. Da Silva, *J. Zool.* **237**, 227 (1993); 4. C. R. Brown, M. Bomberger Brown, S. A. Raouf, L. C. Smith, J. C. Wingfield, *Ecology* **86**, 2904 (2005); 5. J. R. Belthoff, A. M. Dufty, *Anim. Behav.* **55**, 405 (1998); 6. A. Trefilov, J. Berard, M. Krawczak, J. Schmidke, *Behav. Genet.* **30**, 295 (2000); 7. N. J. Dingenmase, C. Both, A. J. van Nordwijk, A. L. Rutten, P. J. Drent, *Proc. R. Soc. Lond. B* **270**, 741 (2003); 8. T. Ebenhard, *Oikos* **49**, 297 (1987); 9. J. H. Myers, C. J. Krebs, *Ecol. Monogr.* **41**, 53 (1971); 10. J. Cote, J. Clobert, *Proc. R. Soc. Lond. B* **274**, 383 (2007); 11. P. Abbot, J. H. Withgott, N. A. Moran, *Proc. Natl Acad. Sci. U.S.A.* **98**, 12068 (2001); 12. R. A. Ims, *Oikos* **57**, 106 (1990); 13. R. A. Duckworth, A. V. Badyaev, *Proc. Natl Acad. Sci. U.S.A.* **104**, 15017 (2007); 14. M. J. O'Riain, J. U. M. Jarvis, C. G. Faulkes, *Nature* **380**, 619 (1996); 15. K. E. Holekamp, *Ecol. Monogr.* **56**, 365 (1986); 16. B. Sinervo, R. Calsbeek, T. Comendant, C. Both, C. Adamopoulou, J. Clobert, *Am. Nat.* **168**, 88 (2006); 17. E. J. Fjerdingstad, N. Schtickzelle, P. Manhes, A. Gutierrez, J. Clobert, *BMC Evol. Biol.* **7**, 133 (2007); 18. I. Hanski, A. Peltonen, L. Kaski, *Oikos* **62**, 48 (1991); 19. B. R. Anholt, *Oecologia* **83**, 385 (1990); 20. L. K. Wahlstrom, O. Liberg, *J. Zool.* **235**, 455 (1995); 21. C. Barbraud, A. R. Johnson, G. Bertault, *J. Anim. Ecol.* **72**, 246 (2003); 22. I. Hanski, M. Saastamoinen, O. Ovaskainen, *J. Anim. Ecol.* **75**, 91 (2006); 23. T. Ebenhard, *Ecology* **71**, 1833 (1990); 24. D. A. Roff, D. J. Fairbairn, in *Dispersal*, J. Clobert, E. Danchin, A. A. Dhondt, J. Nichols, Eds. (Cambridge University Press, 2001).

Denno 1997). The second scenario is well illustrated by the trade-off between dispersal potential and competitive ability in insects (Roff & Fairbairn 2001) and has also been hypothesized to occur in small mammals (Ebenhard 1990).

Selection might also promote phenotypic adaptations that mitigate the costs of dispersal and/or facilitate settlement, ultimately equalizing inclusive fitness between dispersers and residents. There is good empirical evidence that dispersal involves a variety of costs during transience and at settlement (e.g. Bonte *et al.* 2006; Schtickzelle *et al.* 2006). It is also increasingly apparent that selection on some phenotypic traits (e.g. body condition) and behaviours (e.g. boldness, aggressiveness) can act to reduce these costs (O'Riain *et al.* 1996; Barbraud *et al.* 2003; Duckworth 2006; Sinervo *et al.* 2006). Such benefits could potentially arise at all steps of the dispersal process and might be acquired through phenotypic modifications that confer survival and/or fecundity advantages to dispersers (Bélichon *et al.*

1996). Within the same species, a suite of traits that decrease the costs of dispersal and benefit dispersers can combine to produce a *dispersal type*, such as the morphological and behavioural syndromes of dispersers in the naked mole rat (O'Riain *et al.* 1996). In this species, dispersers from laboratory colonies are both larger and fatter than residents and the former also exhibit mating preferences towards non-colony members. In other mammals, such as Belding's ground squirrels or grey-sided voles, dispersal is initiated by an ontogenic switch that also triggers the expression of a large syndrome of behaviours, including exploration, loco-motor activity and boldness (Holekamp 1986; Ims 1990).

We currently lack a conceptual framework to explain the emergence of phenotype-dependent dispersal, which is a form of intraspecific polymorphism between the dispersing and resident strategies. At the between-species level, however, a growing number of models have been con-structed to investigate joint selection on dispersal behaviour

and other life-history traits. These models predict significant correlated responses to selection on dispersal and a variety of traits, including reproductive effort (Pen 2000), senescence (Dytham & Travis 2006), mate choice and inbreeding avoidance (Lehmann & Perrin 2002), and altruistic behaviours (Le Galliard *et al.* 2005). To illustrate this, Le Galliard *et al.* (2005) have shown by means of adaptive dynamics models that selection against dispersal due to higher dispersal costs often promotes selection for higher cooperation, thus favouring negative evolutionary correlations between the two traits. The scenario prevalent in these models is that correlational selection should result in dispersal types determined by robust genetic correlations between dispersal behaviour and other phenotypic traits (Sinervo *et al.* 2008). Such correlations can be difficult to quantify for complex behavioural traits like dispersal (Roff & Fairbairn 2001), but evidence does exist in ciliates, wing-dimorphic insects, and also one bird species that some life history, behavioural and morphological traits are genetically correlated with dispersal (Table 1). For example, a candidate gene for dispersal has been identified in the butterfly *Melitaea cinxi* by Haag *et al.* (2005) and this gene plays an important role in controlling flight metabolism.

In contrast, other experiments have highlighted the important role of the environment in inducing dispersal types either through direct behavioural effects (Table 2) and/or through indirect developmental effects (reviewed in Dufty *et al.* 2002). We argue that this phenotypic plasticity should be a common feature. Indeed, dispersal is a common response to several forms of habitat degradation – including predation, parasitism, shortage of mates and competition with conspecifics and kin – that do not necessarily involve the same costs and benefits. Thus, we expect phenotypic adaptations in dispersers to depend upon the factors that motivate dispersal. First, all phenotypic traits do not confer an equal ability to cope with all sources of habitat degradation. For example, sensitivity to competition with conspecifics may depend upon resource holding potential affected by size and age, while sensitivity to shortage of mates is more likely to depend upon sex and mating skills influenced by exploration capacity and attractiveness. Second, factors promoting the evolution of dispersal do not display the same spatial heterogeneity, and therefore require different dispersal distances and phenotypic adaptations. For example, escaping kin competition or inbreeding typically requires a move of only a short distance while escaping competition with non-relatives or a food shortage within the habitat patch might require a much longer dispersal distance and therefore a greater movement ability (Stenseth & Lidicker 1992). Third, the relative benefits of

Table 2 Case examples of external factors causing phenotypic differences between dispersers and residents or among settlers

External factors	Observed dispersal pattern	Reference
Kin competition	Daughter–daughter competition is associated with dispersal by heavier individuals in red-backed voles	(1)
	Mother–offspring competition causes dispersal by fatter juvenile common lizards	(2)
	Kin competition among fig wasps influences the body size of male dispersers depending on levels of mate and resource competition	(3)
Intraspecific competition	Dispersing common shrews are larger than residents during the low phase of a small rodents population cycle, but not during peak years	(4)
	Dispersing male meadow voles are more aggressive than residents during a population peak than during the increasing and declining phases	(5)
	Small male milkweed beetles are more likely to leave host plants with male-biased sex ratios than large males	(6)
	Baseline corticosterone levels influence habitat choice for small or large colonies in cliff swallows	(7)
Habitat quality	Dispersing common mole rats tend to be heavier than residents in arid habitats, but not in mesic habitats	(8)
	Habitat quality and population density determine settlement differentially in small and large adult great tits	(9)
	Habitat type differentially influences habitat choice of bluegills with small and large pectoral fins	(10)

We indicate the observed dispersal pattern for each study but did not find any clear study describing inbreeding risk.
1. M. Kawata, *Oecologia* **72**, 115 (1987); 2. J.-F. Le Galliard, R. Ferrière, J. Clobert, *Proc. R. Soc. Lond. B* **270**, 1163 (2003); 3. J. C. Moore, A. Loggenberg, J. M. Greeff, *Biol. Lett.* **2**, 17 (2006). 4. I. Hanski, A. Peltonen, L. Kaski, *Oikos* **62**, 48 (1991); 5. J. H. Myers, C. J. Krebs, *Ecol. Monogr.* **41**, 53 (1971); 6. W. S. Lawrence, *Behav. Ecol. Sociobiol.* **21**, 367 (1987); 7. C. R. Brown, M. Bomberger Brown, S. A. Raouf, L. C. Smith, J. C. Wingfield, *Ecology* **86**, 2904 (2005); 8. A. C. Spinks, J. U. M. Jarvis, N. C. Bennett, *J. Anim. Ecol.* **69**, 224 (2000); 9. D. Garant, L. E. B. Kruuk, T. A. Wilkin, R. H. McCleery, B. C. Sheldon, *Nature* **433**, 60 (2005); 10. T. J. Ehlinger, *Ecology* **71**, 886 (Jun, 1990).

phenotype-dependent dispersal depend crucially on temporal variation of which patterns of fluctuation should vary between factors that promote dispersal. For example, competition with conspecifics in a randomly fluctuating population is less predictable than inbreeding risks and the expected benefits of producing a specific dispersal type is then likely to be stronger when dispersal is triggered by inbreeding avoidance than when dispersal is triggered by intraspecific competition. These three hypotheses have been poorly investigated so far and could help to explain the observed intra- and interspecific variation in the phenotype of dispersers (Table 1).

Given that both the probability of dispersal and the induction of an appropriate dispersal type should often be context-dependent, the appropriate framework to understand the evolution of dispersal behaviour is to describe the *dispersal reaction norms*. The dispersal reaction norm characterizes the array of dispersal behaviours and dispersal types of a given genotype along an environmental gradient. Whenever some cues about the expected variation in local conditions are available, condition-dependent dispersal and plasticity in phenotype-dependent dispersal are likely to evolve under a wide range of ecological conditions (Bowler & Benton 2005). Phenotypic plasticity in dispersal is even more likely to evolve when individuals can gather information at both local and distant scales, as suggested by the concept of informed dispersal (see below). Furthermore, dispersal is a life-history trait controlled by many developmental and behavioural pathways (Dufty *et al.* 2002). This implies that a simple control of dispersal plasticity through genes with pleiotropic effects is less likely than a control through epistatic gene networks (see Sinervo *et al.* 2008 for a discussion of this issue). In the latter case, it is worth

mentioning that a more rapid re-organization of associations between condition- and phenotype-dependent dispersal in response to environmental changes can be expected. Unfortunately, we lack crucial data on this topic and further quantitative genetic studies are needed to understand the genetic architecture of dispersal plasticity.

To summarize this section, we can draw two general predictions. First, plasticity cannot be perfect and not all genotypes or phenotypes will have an optimal dispersal response to all environmental factors; rather we should observe genotypes or phenotypes that are adapted to deal with some factors more than others. Second, the developmental cascades of gene interactions and hormonal networks that control dispersal should most often be condition-dependent. We should therefore expect to find individual and environmental heterogeneity among dispersers.

HYPOTHESES AND MECHANISMS LINKING DEPARTURE BEHAVIOUR WITH SETTLEMENT STRATEGIES

Even in homogenous landscapes and for passively dispersing organisms, dispersal typically involves the three successive stages of departure, transience and settlement. As such, events occurring at one step might influence decisions taken in subsequent steps (Table 3). For example, individual heterogeneity among dispersers is likely to have carry-over effects during transience. Unfortunately, few data exist on individual heterogeneity during transience and exploration (Haughland & Larsen 2004; Mabry & Stamps 2008). In species with restricted movement ability, the direction and length of movements should be strongly influenced by the natal environment before dispersal or by an interaction

Table 3 Case examples of the cascading effects of behavioural decisions taken during the successive dispersal stages (departure, transience and settlement)

Cascading effects	Observed dispersal pattern	Phenotype	Reference
From departure to transience	Habitat quality in the natal home range influences transience behaviour	No	(1)
	Habitat type influences direction and consistency of transience movements	No	(2)
From departure to settlement	Density in the natal patch influences density-dependent settlement behaviour	No	(3)
	Habitat quality in the natal patch influences subsequent settlement behaviour	Yes (body size)	(4)
		No	(1)
From transience to settlement	Over-wintering habitat influences breeding habitat choice in a migrating passerine	Yes (condition)	(5)

For each study and cascading effect, we indicate the observed dispersal pattern and whether phenotype-dependence was thought to be the factor linking the stages of the dispersal process.
1. K. E. Mabry, J. A. Stamps, *Proc. R. Soc. Lond. B* **275**, 543 (2008); 2. D. L. Haughland, K. W. Larsen, *J. Anim. Ecol.* **73**, 1024 (2004); 3. J. Cote, J. Clobert, *Proc. R. Soc. Lond. B* **274**, 383 (2007); 4. S. Verhulst, C. M. Perrins, R. Riddington, *Ecology* **78**, 864 (1997); 5. C. E. Studds, T. K. Kyser, P. P. Marra, *Proc. Natl Acad. Sci. U.S.A.* **105**, 2929 (2008).

between individuals and their movement vectors. For example, the acantocephalan parasite *Pomphorhynchus minutus* manipulates its intermediate host, the amphipod *Gammarus pulex*, by increasing its attraction towards the water surface where the amphipod has a higher chance of being predated by birds, the final host, which facilitates dispersal to another pond (Cézilly *et al.* 2000). Few studies have investigated the interaction between departure factors and transience behaviour in species where individuals can control their movements. For example, Lambin (1994) demonstrated that natal dispersal triggered by inbreeding avoidance in Townsend's voles caused males and females to move in opposite directions during transience. In a recent and unique example, Dries Bonte *et al.* showed in a spider that the interaction between departure factors and exploration movement was far more complex than initially thought. To disperse as an adult, this species can either rappel towards a nearby plant or balloon with silk threads to a more distant one (Bonte *et al.* 2007). The decision to explore via ballooning or rappelling is triggered by different thermal conditions experienced during juvenile life (Bonte *et al.* in press).

Conditions experienced in the departure patch may also influence the future settlement strategies of dispersers. There is a vast theoretical and empirical literature on breeding habitat selection. Unsurprisingly, similar factors form the basis of habitat selection and dispersal decisions, and individual heterogeneity in behaviour has been recorded in the context of breeding habitat selection (Stamps 2001). For example, kittiwakes, a colonial sea bird, choose their future breeding sites by cuing on the reproductive success of conspecifics when they themselves failed to breed, but use the same site when previously successful breeders (Danchin *et al.* 1998). In other species, habitat choice strategies depend also upon individual phenotype and past life history. In the colour polymorphic side-blotched lizard (*Uta stansburiana*), adult males are either attracted or repulsed by the presence of genetically similar individuals (Sinervo & Clobert 2003) depending on their territory holding strategy (cooperative or aggressive) and kin structure (Sinervo *et al.* 2006).

Whether there are interactions between factors involved in departure decisions and settlement strategies is thus an interesting question to explore. The sequential nature of the behavioural stages of dispersal makes it likely that decisions taken during one stage can influence the costs and benefits of decisions taken in the next stage (Fig. 1 and Table 3). On the one hand, local conditions might act as an early determinant of the phenotype of dispersers and therefore of their subsequent habitat choice strategies. This scenario was investigated by Stamps (2006) in the context of a silver spoon effect on habitat selection, where dispersers born in high-quality patches are more likely to settle in good-quality

habitats than dispersers from bad-quality patches. We argue that the production of plastic dispersal phenotype is in fact a general mechanism linking departure decisions with the future breeding habitat selection strategies of dispersers, of which the silver spoon effect is one example. The production of a special phenotype that enhances dispersal success will often result in biasing habitat selection of dispersers towards those habitats that best match this specialized phenotype. Thus, a bias in habitat selection strategies of dispersers might only result as a by-product of any phenotypic adaptation that confers an advantage to dispersers in a given context (Benard & McCauley 2008). For example, individuals who experience competition among kin in the common lizard and depart are larger and have better survival in unoccupied habitats (Cote *et al.* 2007).

On the other hand, environments experienced before departure and during transience might influence the settlement behaviour of dispersers irrespective of their phenotype. This could be the case when prior-knowledge of the habitat is so critical to reproductive success that familiarity is used as a cue to select a breeding habitat (Davis & Stamps 2004). For example, in red squirrels, familiarity with the natal and exploration habitat is a predictor of habitat preferences during settlement, such that juveniles tend to settle preferentially in more familiar habitats irrespective of their intrinsic quality (Haughland & Larsen 2004). Proximate factors involved in departure from the natal or breeding area, however, may not always interact with the settlement decisions. Kin competition or inbreeding can be avoided by moving a few patches away from the parental territory, and it is difficult to see how these causes can act directly later in life on habitat choice of dispersers when relatives are no longer present. We anticipate that a link between departure and settlement decisions is more likely for habitat quality and density dependence as these factors are involved in both sides of the dispersal process (Clobert *et al.* 2004; Stamps 2006; Benard & McCauley 2008). For example, insects developing on a given host plant will often search for other similar hosts on which to lay their eggs when sexually mature (Hanski & Singer 2001) – a process known as habitat matching or natal habitat preference induction (Davis & Stamps 2004). Intraspecific competition might be as important a factor as habitat quality in linking departure and settlement decisions through density-dependence emigration and immigration (Cote & Clobert 2007). Most attempts to understand habitat choice strategies have been conducted without accounting for individual variation in departure or transience behaviours. This should, however, be feasible by measuring environmental variation in the source and settlement habitats or by experimentally manipulating habitat quality in the departure and settlement patches.

INFORMED DISPERSAL: INTEGRATING CUES TO PRODUCE AN OPTIMAL DISPERSAL BEHAVIOUR

Phenotypic plasticity in dispersal strategies requires a strong ability to gather and process information. Information use should therefore be a key process when animals attempt to move between habitats as already demonstrated for foraging movements (Valone 1989). Here, we propose the concept of 'informed dispersal' to encapsulate the idea that individuals gather and exchange information at the different stages of dispersal. The concept of informed dispersal increases our understanding of how and why some individuals use certain cues during dispersal. It also implies that movements involve not only an exchange of individuals between patches of habitat, but also information transfer through the landscape (Cote & Clobert 2007).

Information use during dispersal can be best understood by analysing the properties of the emitter (cue) and receptor (individuals) system that underpins communication. Broadly speaking, emitters can consist either of cues that behave passively or actively towards the receptors *sensu* Danchin *et al.* (2004). To orientate during movements, most animals use landscape landmarks or other abiotic cues, which are all passive non-social emitters (e.g. Naylor 2006). For example, nocturnal snakes choose thermally suitable habitats through the physical structure and temperature of rocks (Webb *et al.* 2004). The knowledge of such landmarks is not necessarily acquired directly by all individuals, and some individuals may copy others to find their way through the landscape (Couzin *et al.* 2005). Indeed, conspecifics can serve as an important source of social information with respect to dispersal decisions (Danchin *et al.* 1998). Individuals may assess environmental quality through the presence of conspecifics without themselves paying the costs of detailed exploration, such as occurs when Luschan's salamanders use chemical scents deposited by conspecifics to identify a safe shelter (Gautier *et al.* 2006). Individual heterogeneity in information use can be generated by differences in individual quality, life histories or genetic background and is likely to maintain large variations in dispersal strategies (e.g. Massot *et al.* 2002).

Social information can take forms other than the simple presence of conspecifics. Individuals may acquire information about their environment through the morphology, behaviour or even reproductive success of conspecifics (Danchin *et al.* 2004; Doligez *et al.* 2004; Dall *et al.* 2005). Social information is often considered to be a cost-free and effective means of deciding when to disperse (Dall *et al.* 2005). However, the meaning of the information conveyed by the presence of conspecifics (intraspecific competition or habitat quality) is likely to be ambiguous at times and triggered by interactions with other sources of public or private information (Danchin *et al.* 2004). Sensitivity to a particular cue should essentially be governed by the pattern of temporal autocorrelation, but also, in the case of dispersal, by the spatial range at which this autocorrelation occurs. When and to which environmental cue an individual should be sensitive depends on the age-specific reproductive values and temporal autocorrelation in the cue (Ims & Hjermann 2001; Clobert *et al.* 2004). However, how individuals integrate information from several cues in order to make appropriate dispersal decisions is challenging. There is a need to search for both the proximate mechanisms and the evolutionary rules that are used to integrate multiple and potentially conflicting sources of information.

Organisms with a limited capacity to explore their surroundings prior to dispersal have to rely on information in their resident population to decide whether or not to disperse. Residents and dispersers differ in a variety of morphological, behavioural and life-history traits (Tables 1 and 2). The presence and type of immigrants may therefore themselves serve as cues for the dispersal behaviour of their conspecifics, as in fact has been shown in a species of small ground-dwelling lizard. Common lizards are able to distinguish between residents and dispersers and can acquire information about the density of surrounding populations through some unknown traits of immigrant lizards (Cote *et al.* 2008). Individuals use social information derived from the presence and characteristics of these immigrants in their decision to disperse (Cote & Clobert 2007). If such passive mechanisms to acquire information about the surrounding populations have evolved in animals with limited exploration capacities, dispersal may contribute to an ideal-free distribution of individuals across habitats in far more species than previously thought.

DEMOGRAPHIC CONSEQUENCES OF CONDITION-DEPENDENT DISPERSAL, INFORMATION AND DISPERSAL SYNDROMES

In spatially structured populations, the viability and dynamics of the population depend critically upon dispersal behaviour. Some mechanisms, such as passive and active information acquisition, allow individuals to efficiently track variations in habitat quality. Other mechanisms, such as habitat matching, tend to decrease metapopulation connectivity as some individuals specialize towards a restricted set of environmental characteristics (e.g. Hanski & Saccheri 2006; Benard & McCauley 2008). The evolution of informed dispersal that tends to favour an ideal-free distribution of individuals on the one hand and of specialized dispersal types that are not searching for the optimal habitat at the population level on the other hand can be viewed as opposing forces. Extinction, colonization and invasion processes in spatially structured populations are demographic by-products of these two antagonistic evolutionary processes.

Recent studies have emphasized that heterogeneity among dispersers might explain the long tail of dispersal kernels and therefore species invasiveness (e.g. Fraser *et al.* 2001; Rehage & Sih 2004). In addition, it is well documented that the relative importance of behavioural flexibility and dispersal syndromes may be crucial to the invasion success of a given species (e.g. Duckworth & Badyaev 2007). Indeed, dispersers are likely to form a heterogeneous sample of individuals when dispersal syndromes are cause-dependent and criteria for settlement depend both upon departure and exploration habitats (Tables 1–3). At the population level, there is accumulating evidence that the phenotypic composition of recently colonized populations differs from that of older populations for traits linked with dispersal (Olivieri *et al.* 1995; Hanski *et al.* 2004; Duckworth & Badyaev 2007). In turn, these differences in the phenotypic composition of new and old patches of habitat may influence their population dynamics. A combined understanding of dispersal syndromes, causes of departure and information gathering processes might therefore shed new light on the understanding of spatially structured populations and species invasiveness.

A good example of how dispersal syndromes can influence spatial population dynamics comes from studies of metapopulations. Classical metapopulation systems represent an extreme form of patchiness and their dynamics depend both on local extinction, colonization (or rescue) due to dispersal in extinct (or very low density) patches and reinforcement due to dispersal in high-density patches (Hanski 1999). For this reason, it has been suggested that colonization, rescue and reinforcement might not necessarily involve the same individuals (e.g. Wade & McCauley 1988). In the common lizard, for example, individuals differ in social personality (i.e. behavioural attraction towards conspecifics) and social personality predicts whether some individuals disperse to join high-density rather than low-density patches (Cote & Clobert 2007). The existence of a colonization strategy (colonizers) has also been speculated in various species of vertebrates (e.g. Ebenhard 1990; Duckworth & Badyaev 2007). Imagine a metapopulation of joiners that disperse towards extant populations in their surroundings by means of active or passive information gathering (Fig. 2). If no population extinction occurs, a metapopulation of joiners can be viable and evolution should favour the existence of such information gathering processes. If extinction happens regularly, however, colonization might not be feasible due to the settlement behaviour of joiners (Fig. 2a) and the existence of colonizers is then crucial to metapopulation viability (Figs 2b and 3). Such heterogeneity in dispersal behaviour may reflect genetically based morphological or behavioural adaptations (e.g. Hanski *et al.* 2004). In this case, the coexistence of colonizers and joiners will most probably depend on extinction rate, such that the potential for colonization might be very weak in stable habitats. However, as we suggested earlier, there are also non-genetic mechanisms that can generate heterogeneity in dispersal behaviour. For example, kin selection theory predicts that dispersers should engage in risky moves as they trade-off direct fitness costs of dispersal with indirect genetic benefits (Hamilton & May 1977). Indeed, in the common lizard, dispersers leaving a population due to
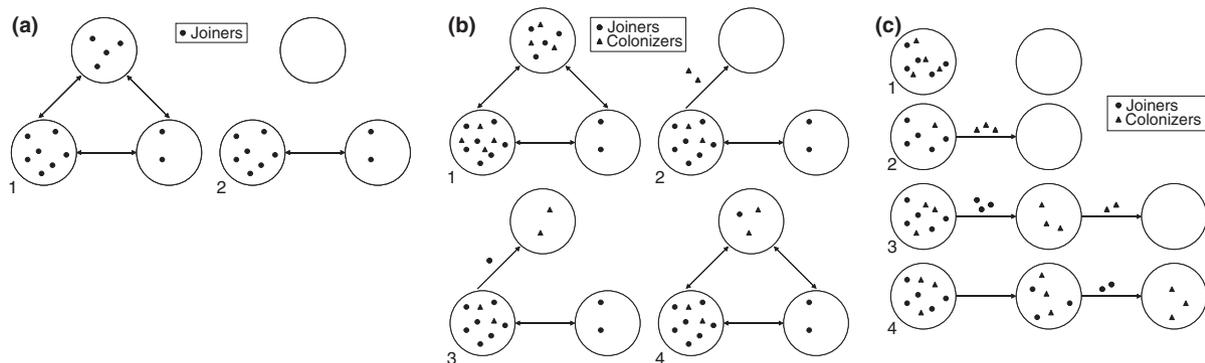

Figure 2 Hypothetical examples of the demographic consequences of heterogeneous dispersal behaviours for metapopulation dynamics. The figures describe two scenarios with only joiners (a) or with joiners and colonizers (b). In (a), when one population goes extinct, there is no recolonization of this population by joiners. In (b), the presence of colonizers allows recolonization of extinct patches and persistence of the entire metapopulation. Similarly, heterogeneity among dispersers can play a crucial role during an invasion and/or range expansion process by speeding up colonization effects (c). In this scenario, colonizers first establish new populations and these pioneer populations are then reinforced by joiners. Eventually, immigration by joiners bring the newly established population towards its carrying capacity. Directed movements and individual heterogeneity in habitat selection are therefore key processes in metapopulation and invasion dynamics.

interactions with close relatives have distinct phenotypes (Table 2) and exhibit a survival advantage in unoccupied habitats (Cote *et al.* 2007). In this case, the equilibrium distribution of dispersal strategies should depend more on the prevalent factor that promotes the evolution of dispersal behaviour and dispersal syndromes than upon metapopulation dynamics. Also, the colonization dynamics would likely be governed by the demographic structure of source populations. When new habitats become available, for example, due to climate change, the capacity of a species to expand or invade (Fig. 2b) will depend upon the populations' structure at the margin of the distribution range (presence of colonizing types) and the dominant dispersal cause acting in those populations.

The above scenario further emphasizes the conflicting nature of the information derived from the presence of conspecifics. For a long time, it was thought that density-dependence dispersal should always be positive as dispersal allows the avoidance of competition. However, negative correlations between dispersal probability and density have been observed in several species (Lambin 1994; Andreassen & Ims 2001; Matthysen 2005). This reverse trend could be explained by an increase in density either rendering dispersal more difficult (more territories to cross) or more costly (higher distance-dependent mortality and lower settlement success). Alternatively, habitats occupied by conspecifics could be preferred over non-occupied habitats when density indicates higher habitat quality, the presence of potential mates for settlers, or lower settlement costs (Stamps 2001; Le Galliard *et al.* 2003). Therefore, density-dependent dispersal itself may be context dependent. Bowler & Benton (2005) have highlighted the population-level consequences of differences in density-dependent dispersal. Yet, we lack a comprehensive framework that link together habitat quality, density-dependence and metapopulation dynamics when dispersal is non-random.

Small vertebrates and arthropods living in fragmented landscapes may prove ideal study systems to investigate the demographic effects of informed dispersal and phenotype-dependent dispersal emphasized here. Earlier studies have found that dispersal behaviour is often context-dependent and can be highly variable among individuals in these species (Table 1). For example, using small mammals in fragmented habitats as a model system, Lambin *et al.* (2004) discovered that flexible dispersal strategies are critical to ensure frequent rescues and colonizations. However, the dispersal syndromes evolved by these species in more continuous habitats may not allow them to persist in secondarily fragmented habitats. Future studies should aim at better understanding the ecological and evolutionary feedbacks between flexible dispersal strategies and spatial population dynamics in naturally or experimentally contrasted landscapes.

SPATIAL SCALES, TIME CONSTRAINTS AND COMMUNITY PROCESSES

The demographic consequences of condition-dependent dispersal should clearly depend on the distance distribution of dispersal movements (dispersal kernel). Departure factors, such as kin competition, density dependence and habitat heterogeneity, are all operating at different scales. The operating scale of departure factors can be small but nevertheless induce long-distance movements. Indeed, the dispersal type most sensitive to a given departure factor might be a more important determinant of the dispersal kernel than the departure factor itself. For example, kin competition and inbreeding avoidance could both produce long distance dispersers through their effects on dispersal types (Table 2), though the operating scale of these departure factors is usually small (Stenseth & Lidicker 1992; Ronce *et al.* 2001).

Species often differ greatly in their dispersal strategies. Different species may use different cues to disperse and we therefore expect contrasted demographic responses to habitat fragmentation, as Fahrig (2003) reported in a comprehensive survey. In addition, some species may have a strong time constraint to disperse (e.g. short-lived species in patchy landscapes) while others have little constraint and can embark in successive dispersal events throughout their life. The degree of time constraints on dispersal will affect to a great extent the rules governing transience and settlement behaviours. Information gathered during the transience (which takes several years in some birds and mammals) when foraging or exploring might strongly diminish the influence of the information gathered at the other stages of the dispersal process. However, the general framework proposed here should be applicable to a variety of life styles and we predict that the relative influence of information gathered at the different stages will be strongly affected by species-specific constraints.

Dispersal decisions might get even more complex in species assemblages. Indeed, species are also likely to leave or settle in a habitat with respect to risks of parasitism, predation or competition with heterospecifics (e.g. Hauzy *et al.* 2007). The relative importance of intra- and interspecific factors should shape the sensitivity of dispersal in one species to the presence of another species, but virtually no work has been carried out on this question. We might hypothesize that, to some extent, interspecific interactions may play a similar role as intraspecific interactions in competitive communities; for example, heterospecifics can serve as dispersal cues such that information exchanges among competitors within a landscape might partly govern the dynamics of metacommunities (Thomson *et al.* 2003). Also, dispersal tactics in predator–prey and host–parasite systems are likely to

depend on which species govern the ecological dynamics (top–down vs. bottom–up control) and on costs to disperse to low predation/parasitism areas, which often are more valuable for the prey/host. For example, prey invest less in predator defence, including avoidance by dispersal, in high-quality than in low-quality environments (van Baalen *et al.* 2001). Furthermore, all phenotypes within a population of a species are not equally affected by interspecific competition, predation or parasitism (and vice and versa). These differential sensitivities should select for species-specific dispersal types (Sih *et al.* 1992) and therefore affect colonization rate and metacommunity dynamics. If such phenotype-dependent dispersal proves true, we recommend that experiments aiming to understand the effects of dispersal on metacommunities or on spatially structured host–parasite/ prey–predator populations should compare situations where dispersal is forced with situations where individuals are allowed to move freely among communities (Cadotte 2007).

CONCLUSION AND PERSPECTIVES

The importance of incorporating individual heterogeneity into ecological thinking has been more fully appreciated in recent years. Some years ago, Bekoff (1977) also realized the importance of accounting for individual variation to understand the nature and evolution of dispersal behaviour in different mammalian social systems. Despite this early work and other pioneering studies, there are still too few attempts to include these considerations into empirical studies and theoretical models of dispersal. Here, we provide an updated review and synthesis of our current understanding of the nature and ecological consequences of individual variation in dispersal behaviour.
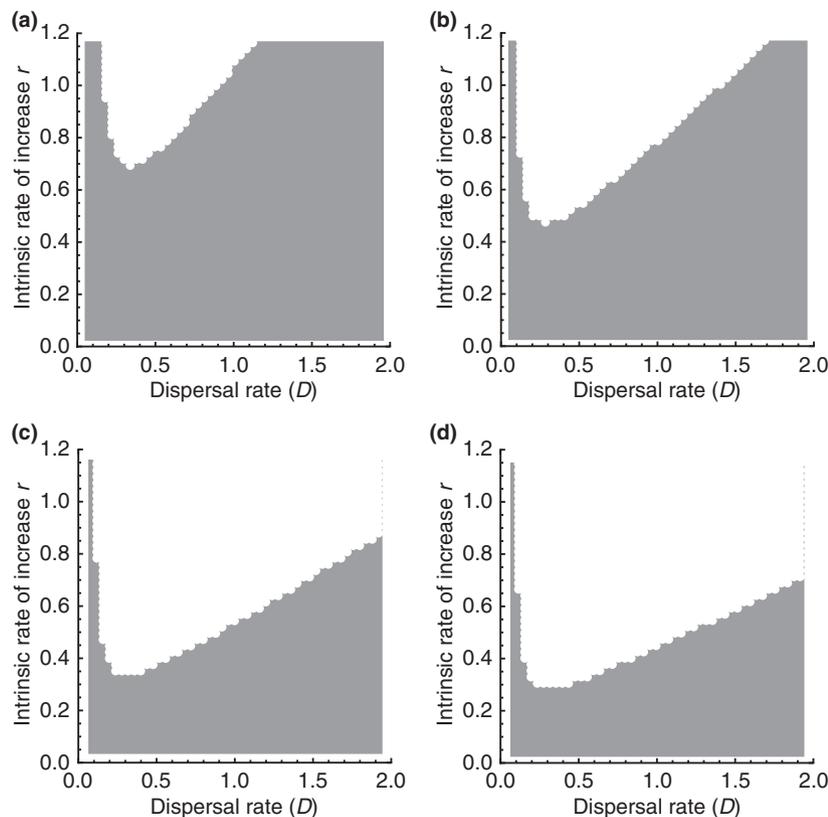

Figure 3 A mathematical analysis of the contribution of heterogeneity among dispersers to metapopulation extinction shows that a higher proportion of colonizers among dispersers (decreases from a to d) can reduce the risk of metapopulation extinction (grey-shaded area) due to demographic and environmental stochasticity. Metapopulation extinction domain is given in the parameter space D (dispersal rate) and r (intrinsic rate of local population increase). The metapopulation model assumes an infinite number of patches, local logistic dynamics, uniform density-independent dispersal and heterogeneity among dispersers. A fixed proportion α of dispersers are colonizers that can only settle in empty patches, while the rest corresponds to joiners that can only settle in occupied patches. Boundaries were calculated with the mesoscale approach advocated by Casagrandi & Gatto (1999) assuming a negative binomial distribution of local abundance. Parameters for calculations were $K = 10$ (carrying capacity), $a = 1$ (no habitat loss), $\beta = 2$ and $\gamma = 0.001$ (local logistic growth) and $h = 0.7$ (clumping parameter). More details on model specification can be found in Casagrandi & Gatto (1999). Proportion of colonizers: $\alpha = 0.50$ (a), $\alpha = 0.70$ (b), $\alpha = 0.90$ (c) and $\alpha = 0.99$ (d).

Our synthesis is based on a qualitative review of the existing literature and some of ideas presented here rely on results obtained with few model systems. Studies of dispersal have been indeed rarely conducted in as much depth as for other life-history traits. Quantifying the concepts described here is therefore the most obvious research priority. We identify four areas where research effort should be directed. First, we need more detailed investigations of condition- and phenotype-dependence in dispersal behaviour. An incredibly large number of studies have focused on age or sexual variation in dispersal behaviour, but we still lack a similar comprehensive treatment of the morphological and behavioural traits that characterize dispersers (Table 1). We urge investigators to make efforts in that direction and report the results of their tests for a variety of phenotypic traits. Second, we need to better understand movement strategies during transience and the way these strategies depend on departure factors and affect subsequent settlement decisions. This should now be feasible both in small-sized species that can be observed in the laboratory or in the field (e.g. arthropods) and with the development of miniaturized devices to track dispersing individuals. Third, we need to understand the proximate mechanisms that underpin dispersal processes. In particular, we encourage researchers to investigate more closely the reaction norms of dispersal behaviour and dispersal-related traits. Finally, we need many more studies that quantify the effects of condition- and phenotype-dependent dispersal on the dynamics of spatially structured populations. These studies could be conducted within the realm of natural ecosystems using a combination of long-term monitoring of dispersal behaviour and individual-based models, or with laboratory organisms in experimental microcosms or meta-populations.

Our synthesis is biased towards studies of dispersal behaviour in terrestrial vertebrates and arthropods, reflecting our own research agenda but also real differences in methods and concepts between plant and animal ecologists and between terrestrial and marine ecologists. Condition- and phenotype-dependent dispersal have been less studied in organisms with 'passive' dispersal mechanisms (see Bonte *et al.* in press). When individuals have weaker behavioural control during transience and settlement, parents could still gather information and control the dispersal type of their offspring as well as choose adequate release conditions. For example, plants can gather information about the level of predation experienced by neighbouring plants (Bruin *et al.* 1995). There are therefore opportunities for these organisms to use available information in order to decrease dispersal uncertainty during transience and settlement, although they will never be able to do it to the same extent than more actively dispersing species.

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GLOSSARY

Dispersal: active or passive attempt to move from a natal/breeding site to another breeding site. Dispersal involves three successive behavioural stages called departure, transience and settlement. Dispersal can occur at any life stage, at any spatial scales above the individual range and within more or less heterogeneous landscapes. Dispersal differs from foraging or migration movements as it implies relocation of the natal/breeding site.

Habitat selection: behavioural processes that result in a biased utilization of habitats and influence the survival and reproduction of individuals; habitat selection can occur at any spatial and temporal scale.

Condition dependence: the observed relationship between external factors and dispersal behaviour at each stage (departure probabilities, movements during transience and settlement probability).

Phenotype dependence: the observed correlation between dispersal behaviour at each stage and other morphological, behavioural and life-history traits in a given population of a given species; this correlation can be caused by genetic and/or environmental factors.

Dispersal syndrome: a suite of characters correlated with dispersal behaviour in a given population of a given species. The dispersal type characterizes the phenotypic attributes of dispersers compared to residents (e.g. dispersers are more aggressive than residents).

Informed dispersal: any dispersal decision based on social or non-social cues.