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BIOLOGICAL

# **Costs of dispersal**

Dries Bonte<sup>1,\*</sup>, Hans Van Dyck<sup>2</sup>, James M. Bullock<sup>3</sup>, Aurélie Coulon<sup>4</sup>, Maria Delgado<sup>5</sup>, Melanie Gibbs<sup>3</sup>, Valerie Lehouck<sup>1</sup>, Erik Matthysen<sup>6</sup>, Karin Mustin<sup>7</sup>, Marjo Saastamoinen<sup>5</sup>, Nicolas Schtickzelle<sup>2</sup>, Virginie M. Stevens<sup>8</sup>, Sofie Vandewoestijne<sup>2</sup>, Michel Baguette<sup>9</sup>, Kamil Barton<sup>10</sup>, Tim G. Benton<sup>11</sup>, Audrey Chaput-Bardy<sup>4</sup>, Jean Clobert<sup>12</sup>, Calvin Dytham<sup>13</sup>, Thomas Hovestadt<sup>10</sup>, Christoph M. Meier<sup>14</sup>, Steve C. F. Palmer<sup>7</sup>, Camille Turlure<sup>2</sup> and Justin M. J. Travis<sup>7</sup>

<sup>6</sup> Evolutionary Ecology Group, Department of Biology, University of Antwerp, Groenenborgerlaan 171, 2020 Antwerpen, Belgium

<sup>9</sup> UMR 7204 MNHN/CNRS/UPMC & Station d'Ecologie Expérimentale du CNRS a Moulis, CNRS, USR 2936, 09200 Saint-Girons, France

<sup>10</sup> University of Wuerzburg, Glashuettenstrasse 5, OT Fabrikschleichach, 96181 Rauhenebrach, Germany

- <sup>11</sup> Faculty of Biological Sciences, Miall Building, Clarendon Way, University of Leeds, Leeds LS2 9JT, UK
- <sup>12</sup> Station d'Ecologie Expérimentale du CNRS a Moulis USR 2936, 14 Moulis, 09200 Saint-Girons, France
- <sup>13</sup> Department of Biology, Wentworth Way, University of York, York, YO10 5DD, UK
- <sup>14</sup> Laboratory of ecological and evolutionary dynamics, Department of Biosciences, Viikinkaari 1, University of Helsinki, Finland

### ABSTRACT

Dispersal costs can be classified into energetic, time, risk and opportunity costs and may be levied directly or deferred during departure, transfer and settlement. They may equally be incurred during life stages before the actual dispersal event through investments in special morphologies. Because costs will eventually determine the performance of dispersing individuals and the evolution of dispersal, we here provide an extensive review on the different cost types that occur during dispersal in a wide array of organisms, ranging from micro-organisms to plants, invertebrates and vertebrates. In general, costs of transfer have been more widely documented in actively dispersing organisms, in contrast to a greater focus on costs during departure and settlement in plants and animals with a passive transfer phase. Costs related to the development of specific dispersal attributes appear to be much more prominent than previously accepted. Because costs induce trade-offs, they give rise to covariation between dispersal and other life-history traits at different scales of organismal organisation. The consequences of (*i*) the presence and magnitude of different costs during different phases of the dispersal process, and (*ii*) their internal organisation through covariation with other life-history traits, are synthesised with respect to potential consequences for species conservation and the need for development of a new generation of spatial simulation models.

Key words: settlement, transfer, departure, trade-offs, fitness, global change, modelling, plants, micro-organisms, invertebrates, vertebrates, marine, aquatic, terrestrial, movement.

<sup>&</sup>lt;sup>1</sup> Ghent University, Dept. Biology, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium

<sup>&</sup>lt;sup>2</sup> Universite catholique de Louvain, Earth and Life Institute, Biodiversity Research Centre, Croix du Sud 4, B-1348 Louvain-la-Neuve, Belgium

<sup>&</sup>lt;sup>3</sup> NERC Centre for Ecology & Hydrology, Maclean building, Benson Lane, Crowmarsh Gifford, Wallingford, OX10 8BB, UK

<sup>&</sup>lt;sup>4</sup> UMR 7179 MNHN/CNRS, Département Ecologie et Gestion de la Biodiversité, Muséum National d'Histoire Naturelle, 4 avenue du Petit Château, 91800 Brunoy, France

<sup>&</sup>lt;sup>5</sup> Metapopulation Research Group, Department of Biosciences, Viikinkaari 1, University of Helsinki, Finland

<sup>&</sup>lt;sup>7</sup> School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

<sup>&</sup>lt;sup>8</sup> F.R.S.-FNRS, Unité de Biologie du Comportement, Université de liège, 22 quai van beneden, 4020 Liège, Belgium

<sup>\*</sup> Address for correspondence (E-mail: Dries.Bonte@ugent.be; Tel: +32 9 264 5213; Fax: +32 9 264 8794).

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## I. INTRODUCTION

Dispersal encompasses all movements of individuals or propagules with potential consequences for gene flow across space (Ronce, 2007). Even though dispersal is an elementary driver of ecological and evolutionary patterns, it remains unresolved which ultimate factors most influence variation of dispersal in natural populations. Wide recognition is given to benefits and costs due to spatio-temporally changing environments, kin competition and inbreeding avoidance (Cressman & Krivan, 2006; Gandon, 1999; Gandon & Michalakis, 1999; Krivan, Cressman & Schneider, 2008; Leturque & Rousset, 2002; Palmqvist, Lundberg & Jonzen, 2000). While all these factors simultaneously shape the process of dispersal, each may influence dispersal in different ways (Lecomte et al., 2004; Stenseth & Lidicker, 1992). This "multi-causality" has hampered progress in disentangling and quantifying the relevance of each factor for dispersal.

A conceptual approach which has proven fruitful is to shift from a population dynamical perspective, with emigration and immigration as the population-level processes, towards an individual-based perspective where dispersal is considered as a multi-phase life-history process. This process can then be considered as composed of traits related to departure (initiation of the eventual act of leaving natal habitat), transfer (movement), and settlement (finalization of the movement phase in novel habitat) (Clobert *et al.*, 2009). The movement phase is often the only component observed in natural conditions, but habitat selection after transfer is becoming recognised as important (Mabry & Stamps, 2008). Departure and settlement are instant behaviours triggered by informed decisions (Clobert *et al.*, 2009). Splitting up the process allows a better understanding of how fitness costs might be levied at each phase, identification of whether levied costs are paid immediately or deferred, and how this affects selection on particular aspects of dispersal (short-long distance, density dependence, sex-biases, etc.). An overview of costs incurred during dispersal is, to the best of our knowledge, lacking and deserves special attention because of its relevance for both fundamental evolutionary biology and applied spatial ecology (e.g. the management of species, communities, ecosystem services and functioning). Many studies have indicated that evolution of life history and dispersal in particular may occur on ecological timescales (e.g. Carroll et al., 2007; Friedenberg, 2003; Cheptou et al., 2008). This suggests that environmental change will create selection on dispersal by modifying its costs and benefits.

Many dispersal-related traits are related to the development of machinery (morphology, physiology) during earlier life, either through plasticity or standing variation in investment (Dingle, 1996). These costs are then incurred during the pre-departure phase (although they may be deferred to later in the life history as well). During development, organisms may invest in phenotypes that enable or enhance their ability to move, e.g. development of wings, or seed adaptations which facilitate attachment to mobile vectors. Since these costs are incurred during development, they are also paid by individuals that eventually stay in the natal habitat. This will by definition contrast with the costs levied during the effective dispersal phase, where costs may be (a) linked to the movement itself (e.g. as a function of distance) taking place during the transfer phase,

or (b) a threshold function of leaving the natal area or entering a new one, being in these cases related to the departure or the settlement phases respectively. We provide a schematic overview describing how the investment in dispersal and the costs paid during dispersal may impact upon investment during development (before dispersal) and also after settlement (Fig. 1).

Dispersal costs will also inevitably feedback against the costs of being or remaining resident (Baguette & Van Dyck, 2007; Belichon, Clobert & Massot, 1996). For instance, increasing the dispersal costs would be expected to decrease dispersal rates. This will lead to lower emigration rates and may increase resource competition, kin competition and inbreeding in local populations. The eventual dispersal strategy will therefore be influenced not only by the costs and benefits of individual decisions but also by frequency-dependent processes at the metapopulation level (Del Mar Delgado *et al.*, 2011).

The selection of different dispersal strategies may be essential for the persistence of populations in fragmented landscapes (Kokko & Lopez-Sepulcre, 2006), and can play a key role in determining the range-expansion dynamics of invasive species and range-shifting in response to climate change (Burton, Phillips & Travis, 2010; Levin *et al.*, 2003). Therefore, the improvement of our knowledge of dispersal

cost structures and covariation with other life-history traits is essential to understand, predict and manage the future of populations. This implies not only the study of energetic and mortality costs during the process of moving between patches, but also of those that are levied before and after settlement, as well as the complex trade-off relationship between them (Fig. 1). We first describe a general framework of dispersal costs with an overview of the main cost types at each of the dispersal phases. Secondly, we present an extensive overview of dispersal costs and their measurement (currencies) among a wide range of organisms. Thirdly, we focus on how these different cost structures may trade-off and feedback against other life-history traits. We elaborate finally on the significance of variation in costs for evolutionary responses to global change and discuss the consequences for future modelling work.

Our review is based on an extensive literature search using the *Web of Science* database for a wide array of taxonomic groups including plants, micro-organisms, terrestrial and marine arthropods, molluscs and bivalves, fishes, reptiles, amphibians, birds and mammals. The search was based on general key search terms: (dispers\* or migrat\* or move\*) and (cost\* or mortality or trade-off\* or fecundity or survival). These search terms rendered more than 11000 papers. Based on the primary criterion that the study effectively dealt with



**Fig. 1.** An individual's life history is shaped by a range of trade-offs (black arrows) as resources cannot be simultaneously invested in growth, reproduction and dispersal. Similarly, investment in resources in one stage of development may be traded-off against other stages: e.g. investment in juvenile growth may be traded-off against adult fecundity. Hence, the investment in dispersal and the costs paid during dispersal may impact upon investment during development (before dispersal) and also after settlement. The process of dispersal is a sequence of "departure, transfer and settlement" (grey arrows), and each has its associated costs. Investment in one phase of the process can impact upon the costs levied elsewhere (e.g. the costs of locomotory apparatus may be paid pre-departure by taking resources away from investment in growth, survival or future fecundity, in which pre-departure costs can impact on post-settlement life history).

dispersal and shows evidence of costs, we here synthesised information from more than 300 papers.

### **II. ORGANISATION OF DISPERSAL COSTS**

#### (1) Cost types and currencies

Despite the fact that costs of dispersal are diverse, no attempt has been made to classify them. In this review, we separate the energetic, time and risk costs from indirect opportunity costs. Energetic and time costs relate to investments that cannot be invested in other activities, while risk costs refer to the probability of dying or suffering harm during dispersal. We define opportunity costs as being related to the surrender of advantages derived from prior residence and familiarity. These costs typically come into play once the organism has left a local area, so after the departure and transfer phase. In this sense, local adaptation can also lead to an opportunity cost as the disperser may lose the advantage of being locally adapted, which has developed through natural selection over former generations. Exact definitions of the costs associated with dispersal are provided in Table 1. All costs can be incurred immediately or subsequently in life, so they can be either direct or deferred. A considerable overlap between both may occur. For instance, a reduction of immunodefence due to energetic expenditure during dispersal can impact on future sensitivity towards diseases (see Table 2).

Table 2 provides examples of the different types of costs. As might be expected, direct and deferred risk and mortality costs are widely documented during the different phases of the dispersal process (Fig 2a: eagle owl mortality during transfer as an example). Risk costs during initiation or during settlement appear, however, to be mostly associated with passively (seeds) or semi-passively (invertebrates) dispersing organisms. Active dispersers may, however, also face such costs by interactions with con- or heterospecifics in the settlement phase due to, for instance, conflicts during territory occupation (Milner et al., 2010; Whitehouse & Jaffe, 1996), but clear evidence within the perspective of dispersal is scarcely documented (but see Griesser et al., 2008; Kahlenberg et al., 2008). Energetic costs are documented for both passively and actively dispersing animals. In the former, energetic costs are related to basal respiration during transfer, while in the latter loss of reserves due to increased locomotory activity are prominent. Costs related to acquired damage (attrition costs) are recorded in animals and plants during transfer, while time costs are sparsely quantified in the light of habitat selection.

Time costs may impact upon opportunity costs that are levied later in life. In a strict sense, it is difficult to link opportunity costs to one specific dispersal phase, and opportunity costs may be directly related to time or energetic costs. For instance, time spent searching for a new habitat is an opportunity cost although it may eventually lead to ultimate benefits in terms of mapping the presence of resources or competitors. In theory the dispersal decisions an individual makes are affected by the expected fitness 'elsewhere' compared to the expected fitness at 'home', although the latter will by definition remain unknown if the individual decides not to disperse (Baguette & Van Dyck, 2007). Therefore individual opportunity costs can be expected to be prevalent in all phases of the dispersal process. The higher predation risk a disperser would face because, for example, it gives up access rights to a defended burrow can be seen as an opportunity cost. However, the higher predation risk of a disperser traversing a hostile landscape matrix is more likely to be a direct cost of dispersal. The time expended during dispersal is a similar case, as it can be considered either as a direct or as an opportunity cost.

One prominent case of opportunity cost that deserves special attention is the loss of evolutionarily acquired advantages when settling in new habitat. Maladaption costs are most obviously incurred at the individual level through immediate decreases of fertility or survival (e.g. Blondel *et al.*, 1993; Bonte *et al.*, 2010*a*; Burt, 1995; Hansson, Bensch & Hasselquist, 2004; Hereford, 2009; Leimu & Fischer, 2008; Vandegehuchte, de la Pena & Bonte, 2010), but can be compensated, for instance, by higher fecundity due to heterozygote advantage and/or reduced genetic load (Agren & Schemske, 1993; Busch, 2005; Mix *et al.*, 2006). Any reduction in fitness at the population level owing to maladaptive genes from immigrants is termed as migration load (Hu & Li, 2003). Burt's study (Burt, 1995) is unique in the

Table 1. Definitions of the different cost types associated with dispersal. All costs can be paid immediately (direct) or in the future (deferred)

Cost type	Definition				
Energetic costs	Costs due to lost metabolic energy in movements. Energetic costs may also comprise costs related to the development of specific machinery associated with dispersal, i.e. energetic expenditure for the construction of special dispersal organs and tissues (muscles, wings).				
Time costs	Direct costs due to the time invested in dispersal that cannot be invested in other activities.				
Risk costs	Direct costs related to both mortality risks (e.g. due to increased predation or settlement in unsuitable habitat) and deferred attrition costs by accumulated damage (e.g. wing wear or wounding) or physiological changes				
Opportunity costs	Costs incurred by selecting the next-best choice available from several mutually exclusive options. Opportunity costs are typical in individuals giving up prior residence advantages and familiarity-related advantages. Opportunity costs also include the loss of any advantage derived from being locally adapted.				

settling in novel underpopulated areas [30, 49, 113]

	Risk	costs					
	Mortality	Attrition	Energy costs	Time costs	Opportunity costs		
Pre-emigration			Cost of wing development in insects [1-5] Behavioural phenotypes with reduced performance [6, 7]				
Initiation	Seed predation [8–15]		Energetic investment for or the production of dispersal structures [17, 22–24]				
	Exposure to predators in arachnids [16, 17] and bivalves [18-21]						
Transfer	Mortality during gut passage in endozoochory [25] Direct predation in microorganisms [26–29], insects [30–33], lizards [34–39] Mortality due to collision [40, 41], road kills [42] and human persecution [41, 43] in vertebrates	Wounding in mammals [44, 45] Trade-offs between movement and immunodefence [46, 47] or disease resistance [48, 49]	Decrease of basal respiration and metabolism in plankton [50–54] Energetic costs of flight [32, 47, 55–58] or ambulatory movements [59–64] in insects, fish [65–68], birds [69–75] and mammals [76–84]				
(Post-) settlement	Post-dispersal seed [85–91]) or seedling predation [92–96] Ending up in bad habitat [97].		Active production of anchoring in marine plankton [21] and aquatic insects [98, 99] Production of chemicals to overcome Allee effects [100]	Search costs to select optimal habitat in birds [101, 102]	Decreased survival [103] or reproductive success [104] in birds due to loss of familiarity with the environment but also due to loss of benefits from nepotism by parents [105–107] Loss of social rank in birds [75, 108–111] and mammals [112] Density-dependent starvation in social or group-living arthropods facing Allee effects when		

Table 2. Examples of the different classes of costs during the pre-emigration, initiation, transfer and (post)settlement phases of dispersal

Table 2. (Cont.)

Risk costs				
Mortality	Attrition	Energy costs	Time costs	Opportunity costs
				Costs of outbreeding depression, by mismatches in the genetic environment, are recorded in song sparrows [114] Loss of local adaptation advantages—migration load [115–119]

References: 1, Dixon & Kindlmann (1999); 2, Denno et al. (1985); 3, Kisimoto (1956); 4, Dixon et al. (1993); 5: Ahlroth et al. (1999); 6, Fjerdingstad et al. (2007); 7, Yano & Takafuji (2002); 8, Xiao et al. (2007); 9, Ostergard et al. (2007); 10, Greig (1993); 11, Traveset (1991); 12, Zagt (1997); 13, Fedriani & Manzaneda (2005); 14, Grimm (1995); 15, Silva & Taberelli (2001); 16, Young & Lockley (1988); 17, Bell et al. (2005); 18, Cummings et al. 1993); 19, Deblok & Tanmaas (1977); 20, Lundquist et al. (2004); 21, Oliver & Retiere (2006); 22, Craig (1997); 23, Vahl & Clausen (1980); 24, Cheung et al. (2006); 25, Vander Wall & Longland (2004); 26, Allen & McAlister (2007); 27, Hiddink et al. (2002); 28, Hiddink & Wolff (2002); 29, Pechenik (1999); 30, Aukema & Raffa (2004); 31, Korb & Linsenmair (2002); 32, Srygley (2004); 33, Galeotti & Inglisa (2001); 34, Amo et al. (2007); 35, Bonnet et al. (1999); 36, Hamann et al. (2007); 37, Jessop et al. (2004); 38, Pietrek et al. (2009); 39, Winne & Hopkins (2006); 40, Smallwood et al. (2009); 41, Real & Manosa (2001); 42, Massemin et al. (1998); 43, Kenward et al. (1999); 44, Solomon (2003); 45, Soulsbury et al. (2008); 46, Adamo et al. (2008); 47, Srygley et al. (2009); 48, Adamo & Parsons (2006); 49, Calleri et al. (2006); 50, Bennet & Marshall (2005); 51, Crawford (1992); 52, Epp & Lewis (1984); 53, McHenry & Patek (2004); 54, Wendt (2000); 55, Combes & Dudley (2009); 56, Berrigan (1991); 57, Hedenstrom et al. (2001); 58, Srygley & Ellington (1999); 59, Kram (1996); 60, Kramer & McLaughlin (2001); 61, Berrigan & Lighton (1994); 62, Full & Tullis (1990); 63, Duncan & Crewe (1993); 64, Lighton et al. (1993); 65, Aarestrup et al. (2005); 66, Cooke et al. (2006); 67, Rand & Hinch (1998); 68, Rand et al. (2006); 69, Bowlin et al. (2005); 70, Johnson et al. (2006); 71, Mandel et al. (2008); 72, Masman & Klaassen (1987); 73, Pennycuick & Desanto (1989); 74, Schnell & Hellack (1979); 75, Vanderwerf (2008); 76, Boldt & Ingold (2005); 77, Davis & Weihs (2007); 78, Fish et al. (2001); 79, Girard (2001); 80, Guerra & Ades (2002); 81, Johnson et al. (2002a); 82, Johnson et al. (2002b); 83, Pontzer (2007); 84, Rosen & Trites (2002); 85, Blate et al. (1998); 86, Cochrane (2003); 87, Farnsworth & Ellison (1997); 88, Forget (1992); 89, Keith & Pellow (2005); 90, Kiviniemi (2001); 91, Nystrand & Granstrom (2000); 92, Edwards & Crawley (1999); 93, Green & Juniper (2004); 94, Hoshizaki et al. (1997); 95, Lopez & Terborgh (2007); 96, Pywell et al. (2007); 97, Cheptou et al. (2008); 98, Fingerut et al. (2009); 99, Fingerut et al. (2006); 100, Huang et al. (2007); 101, Hinsley (2000); 102, Part (1995); 103, Brown et al. (2008); 104, Part (1991); 105, Dickinson et al. (2009); 106, Griesser & Ekman (2004); 107, Nystrand (2007); 108, Forero et al. (2002); 109, Hansson et al. (2004); 110, Nilsson (1989); 111, van der Jeugd (2001); 112, Cant et al. (2001); 113, Bilde et al. (2007); 114, Marr et al. (2002); 115, Blondel et al. (1993); 116, Burt (1995); 117, Leimu & Fischer (2008); 118, Sanford & Kelly (2010); 119, Tack & Roslin (2010).

sense that migration loads in a plant species were estimated to be of a higher magnitude than mutation loads. As such, migration load may equally prevent adaptive divergence (Blackledge & Gillespie, 2004; Gavrilets, Li & Vose, 2000; Hendry, Nosil & Rieseberg, 2007; Hendry & Taylor, 2004; Rasanen & Hendry, 2008), but these costs are not further explored herein since we aim to focus on the individual-level costs rather than those at higher organisational levels.

Costs are manifested through changes in fitness-related parameters. In Table 3 we give an overview of the different types of costs and currencies measured, for the different taxa and different phases of the dispersal process. As expected, most studies have recorded direct measurements of fitness components such as fecundity and survival. Costs specifically related to the development of dispersal-related structures or behaviours are traded-off against reproduction or fecundity (Fig 2b: seed dimorphism as an example). Energetic costs that feedback against fitness in later life phases are also documented for transfer, but here direct survival costs are equally prominent. When damage arises during transfer, costs can be expressed later. Currencies for settlement costs are measured directly in terms of survival and reproduction. Migration or genetic load can be considered as a currency for the loss of opportunity from the point of view of the immigrant, although they are expressed at the population rather than individual level (Burt, 1995) with consequences for the entire 'accepting' population. In birds, opportunity costs have been detected in terms of the loss of social dominance in a new environment (van der Jeugd, 2001).

#### (2) Difficulties in measuring phase-specific costs

Many correlative studies have inferred dispersal costs by comparing fitness-related parameters between philopatric and dispersing individuals (e.g. Belichon et al., 1996). These studies predominantly comprise radio-tracking and capturemark-release studies of larger vertebrates (e.g. mammals: Boldt & Ingold, 2005; Gillis & Krebs, 2000; Gustine et al., 2006; Klar, Herrmann & Kramer-Schadt, 2009; birds: Forsman et al., 2002; Kenward, Marcstrom & Karlbom, 1999; Mandel et al., 2008; Wiens, Noon & Reynolds, 2006; Williams et al., 2000), but also of arthropods (grasshoppers and butterflies; Heidinger et al., 2009; Hein et al., 2003; Schtickzelle & Baguette, 2003). Although all studies assume that these costs are levied during transfer, this is only certain for those studies which explicitly demonstrated mortality during transfer (e.g. traffic kills in red foxes Vulpes vulpes; Soulsbury et al., 2008). In most of the other studies comparing fitness between residents and dispersers, it was not possible to trace the exact origin of the costs.

Selection against dispersal on islands and other isolated populations of passively dispersing organisms has been largely explained in terms of transfer costs (e.g. plants: Colas, Olivieri & Riba, 1997; Fresnillo & Ehlers, 2008; Riba *et al.*, 2009; spiders: Bonte, Bossuyt & Lens, 2007; Bonte *et al.*,



**Fig. 2.** Costs of dispersal. Left: survival costs during natal dispersal in Eagle owls (*Bubo bubo*) (picture by Vincenzo Penteriani); right: heterocarpy in action in *Senecio jacobaea*, with seeds carrying pappus (red arrow) structures being smaller and less viable than those without pappus (blue arrow; picture kindly provided by Bram D'Hondt).

2006, 2003). We are, however, only aware of one study using an island system in which selection against dispersal has been related to costs from settling in non-suitable habitat (Cheptou *et al.*, 2008). By analysing patchy populations of the weed *Crepis sancta* in the city of Montpellier, Cheptou *et al.* (2008) found strong selection against wind-dispersing seeds which had a 55% lower chance of settling in habitable patches on pavements compared with non-dispersing seeds. This led to rapid evolutionary loss of wind-dispersal structures in 5-12generations.

Similarly, a clear population genetic structure in those organisms with an assumed global dispersal suggest that costs of transfer indeed do exist (micro-organisms: Birkemoe & Leinaas, 1999; Lachance, 2004; Ramette & Tiedje, 2007; planktonic marine and freshwater invertebrates: Blanckenhorn, 1994; Matsuo, 2006; Musolin & Numata, 2004; Olafsson, Peterson & Ambrose, 1994). These costs may however, also follow settlement due to genetically or environmentally unsuitable habitat, as evidenced for microbial communities (Van der Gucht *et al.*, 2007), higher plants (Soons & Heil, 2002) and marine planktonic macro-invertebrate larvae (Olafsson *et al.*, 1994). As expected, the phase dependency of dispersal costs is most straightforwardly demonstrated by experiments under field or laboratory conditions.

## III. COSTS DURING THE DIFFERENT DISPERSAL PHASES

## (1) Pre-departure

Pre-departure costs are costs arising during development to enable dispersal. In passively dispersing organisms, examples include investment into special dispersal morphologies such as wings or floating seeds, or fleshy fruits that attract vertebrate dispersal agents. Two other examples comprise the development of specific morphologies in snails enhancing their capacity for drifting (Canete et al., 2007) or free-living planktonic life stages (Pechenik, 1999). These investments involve energetic costs that may eventually reduce fitness, but no empirical quantifications have been found in the literature. This is often due to the lack of adequate controls such as phylogenetic contrasts with species having and lacking the investment, or intraspecific polymorphisms with some individuals making the investment while others do not. In actively dispersing organisms, and insects in particular, costs related to genetic polymorphisms or environmentally induced polyphenisms in dispersal morphs are widely documented. Pterygomorphism, i.e. polymorphism in wing development, is widely documented in insects, with a number of comparative analyses of life-history correlates both within and among related species. For example, Dysdercus beetles are r-selected herbivores from ephemerous habitats that are able to allocate resources from flight muscles to reproduction after settlement (Johnson, 1963). However, this allocation is at the cost of increased time to maturity and subsequent mortality risks during the juvenile life stages (Derr, Alden & Dingle, 1981), as has been also demonstrated in bugs (Tanaka & Wolda, 1987), aphids (Conway & Kring, 2004; Dixon & Kindlmann, 1999) and planthoppers (Denno, Douglass & Jacobs, 1985; Dixon, Horth & Kindlmann, 1993; Dixon & Kindlmann, 1999; Kisimoto, 1956). Similarly, comparisons among seed-eating bug species showed a negative correlation between body size and wing formation (Dingle, Blakley & Miller, 1980; Solbreck, 1986; Solbreck & Sillentullberg, 1990) and subsequently increased developmental time. Winged milkweed bugs Lygaeus equestris produced relatively smaller eggs than wingless individuals, generating offspring which were not resistant to starvation, which thus induced transgenerational fitness costs (Solbreck & Sillentullberg, 1990). Similar trade-offs were demonstrated in winged and wingless cricket (Gryllus firmus) morphs (Roff & DeRose, 2001; Roff, Mostowy & Fairbairn, 2002; Roff et al., 1999; Stirling et al., 2001), mediated through changes in hormone titres feeding back on the basal metabolism (Zera & Bottsford, 2001; Zera & Mole, 1994; Zera, Mole & Rokke, 1994).

Table 3. The distribution of records documenting cost currencies (in brackets in the row below the cost type) according to the number of scanned papers (N) recording costs during the specific dispersal phases. We ordered the studies according to large taxonomic groupings. Because opportunity costs cannot be allocated to one specific dispersal phase (see text), we have depicted their specific currencies separately. Only papers explicitly dealing with dispersal (so excluding movement and migration) are considered

			Reproduction	Survival	Developmental time	Inbreeding	Time	Energy spedure	Attrition (wound- ing, parasites)	Loss social domi- nance
Taxon	Dispersal phase	n	(number of offspring)	(mortality)	(time till development)	Genetic load	(time unit)	(Calories)	Number of wounds, parasite load	Social rank
Micro-organisms	Transfer	9		5			1	3		
Plants	Departure	12	1	11						
	Transfer	2	10	1	1					
	Settlement	43	10	32		1		0		
Marine and	Pre-departure	3						3		
invertable	Departure	1		10				1		
invertebrates	Transfer	22	1	19				2		
т. 1	Settlement	2	4.9	0	10			2		
Insects and	Pre-departure	/6	43	3	12			18	_	
arthropoda	Departure	4		2				20	2	
arunopous	Transfer	40		17	1			20	2	
וי, ו ויד	Opportunity	2	0	1.0				2	0	
Fish and reptiles	I ransfer	10	2	13				0	2	
Birds	I ransier	30		22		0		8		
	Opportunity	9	9	1		2	1			1
Mammals	Transfer	9 97	4	+ 6			1	20		1
waiiiiiais	Settlement	4		4			1	20		

Costs can also be paid by males and are often directly behaviourally mediated. For instance, large-winged male crickets (Crnokrak & Roff, 1995, 1998a, b, 2000; Roff, Crnokrak & Fairbairn, 2003) and aphids (Huberty & Denno, 2006; Langellotto, Denno & Ott, 2000; Novotny, 1995; Sack & Stern, 2007) showed a reduction in mating opportunities compared to wingless or short-winged relatives. In the same vein, winged water striders showed reduced striding ability on the water surface, potentially hindering foraging capacity (Goodwyn & Fujisaki, 2007). In conclusion, costs of being winged and able to fly are typically associated with allocation of resources to wings and muscles at the expense of a poorer condition and decreased fecundity. Another cost is longer development time necessary for growing wings, that tradesoff against attractiveness for mating partners (Goodwyn & Fujisaki, 2007).

In species without wing polymorphisms, but with continuous variation in wing or wing muscle development like butterflies and some water striders, costs of fecundity or survival have also been demonstrated (Ahlroth *et al.*, 1999; Gu & Danthanarayana, 1992; Gu, Hughes & Dorn, 2006; Hanski *et al.*, 2004; Karlsson & Johansson, 2008; Marden & Chai, 1991). Even when dispersive phenotypes are behaviourally rather than morphologically determined, similar patterns of reduced performance in

dispersive phenotypes have been recorded. For instance, in the ciliate *Tetrahymena thermophila* strains may differ in life history, including short-distance dispersal rate and the frequency of producing dispersal morphs. The strains with the dispersive morph carry pre-departure costs reflected in decreased growth (Fjerdingstad *et al.*, 2007). In mites with morphs varying in dispersal propensity, artificial selection experiments have demonstrated a strong negative impact for dispersers in terms of general performance (Yano & Takafuji, 2002). In vertebrates, no specific pre-departure costs for dispersive phenotypes have been recorded to date.

#### (2) Departure: initiation of the dispersal event

Costs that are strictly related to departure are rarely documented. Although the eventual departure decision may result from information gathering during an individual's lifetime, the onset of dispersal is generally a short-term decision-making action and hence, it is the most difficult dispersal stage to study. In accordance with our outline above, departure costs are related to specific costs at the start of the dispersal process, hence costs involved in decision-making to leave the natal patch. While in many organisms costs associated with the development of specific dispersal attributes are incurred during development, only a few study systems consider the quantification of costs during the departure phase itself. Costs associated with exploring the environment (i.e. time, risk and energy costs), even without actually performing dispersal, should be substantial during the initiation of the dispersal event (Larsen & Boutin, 1994; Young, Carlson & Clutton-Brock, 2005; Young & Monfort, 2009). Although these are obviously very difficult to assess by experimental work, quantification of mortality rates, attrition costs or energetic losses during routine exploratory excursions outside the regular home range might provide insights as to their magnitude.

Plants experience costs at departure if seeds attached to the motherplant are predated and are therefore not removed by animal dispersal vectors. We here deliberately consider the production of fruits as a dispersal adaptation and admit that this may be subject to debate. Fruits of high quality will attract frugivores that not necessarily spread seeds, which affects effective emigration. This consumption of fruits may be continued by insects (Chaves & Avalos, 2006; Greig, 1993; Ostergard, Hamback & Ehrlen, 2007; Sullivan & Kelly, 2000; Traveset, 1991; Xiao, Harris & Zhang, 2007; Zagt, 1997) or vertebrates (Fedriani & Manzaneda, 2005; Garcia et al., 2000; Greig, 1993; Grimm, 1995; McKinney & Tomback, 2007; Silva & Tabarelli, 2001). Consumption should not always incur direct mortality costs. Partial fruit consumption may alternatively decrease fruit attractiveness, rendering dispersal beyond the parental neighbourhood less likely (Christensen & Whitham, 1991; Norambuena & Piper, 2000).

Drifting organisms that aggregate at a specific take-off location for transfer provide interesting examples which show the existence of dispersal costs related to the preparation of the dispersal event. For instance, spiders climb elevated structures in the vegetation to prepare for ballooning by tiptoeing (producing silk lines that are used as an airborne sail; Bell et al., 2005). By doing so, spiders expose themselves to predators and experience mortality or damage costs before and during the departure preparation phase (Young & Lockley, 1988). Interestingly, spiders can have an antipredator behaviour when preparing for dispersal by taking a position that allows for a fast escape by jumping when attacked. This suggests that predation during dispersal preparation may be quite common. Similar departure behaviour has been observed in the spider mite Tetranychus urticae (Bell et al., 2005) and in postlarval marine bivalves climbing up the mud to expose produced byssus threads to water currents (Cummings et al., 1993; Deblok & Tanmaas, 1977; Lundquist, Pilditch & Cummings, 2004; Olivier & Retiere, 2006). Besides the energetic investment for positioning (climbing-up the vegetation or the mud), the production of silk lines or byssus threads is also intrinsically a costly process (Bell et al., 2005; Cheung, Luk & Shin, 2006; Craig, 1997; Vahl & Clausen, 1980). Larval benthic invertebrates from stream pools also use silk threads to increase drift dispersal distances (Fingerut *et al.*, 2009). The production of drifting structures should not only be considered as an investment for transition, but also for settlement since it facilitates colonization of rough substrata (Fingerut, Hart & McNair, 2006).

## (3) Transfer

#### (a) Transfer costs in passively dispersed organisms

Endozoochory is the process by which seeds are dispersed by an animal vector, mostly after passage through the gut, but also by regurgitation. Gut passage may impose serious costs of dispersal when passage time is either too long or too short, so that seeds are respectively consumed or not sufficiently affected to allow germination (Cosyns *et al.*, 2005; Traveset *et al.*, 2003; Traveset, Rodriguez-Perez & Pias, 2008). Similarly, when seeds are secondarily dispersed, e.g. by dung beetles or ants, costs could be higher due to suppressed germination at large soil depths (D'Hondt *et al.*, 2008). However, costs can be reduced, for instance due to escape from seed predators after burial, enhanced germination in nutrient-rich sites (Christianini & Oliveira, 2010; Vander Wall & Longland, 2004) or increased directedness towards suitable habitat (Schupp, Jordano & Gomez, 2010).

Many empirical studies of micro-organisms showed costs associated with transfer. The costs are paid because decreasing the basal respiration in the diapause stage during transfer (Bennett & Marshall, 2005; Crawford, 1992; Epp & Lewis, 1984; McHenry & Patek, 2004; Wendt, 2000) comes at the cost of a reduced fecundity (Hall & Colegrave, 2008). In marine plankton, transfer shows deferred costs on post-larval performance (Marshall, Pechenik & Keough, 2003; Pechenik & Cerulli, 1991; Wendt, 1998), increased predation cost because of crossing hostile environments (Allen & McAlister, 2007; Hiddink, Kock & Wolff, 2002; Hiddink & Wolff, 2002; Pechenik, 1999), and mortality due to resource limitation (Horvath & Lamberti, 1999; McConaugha, 1992). Direct mortality costs may be related to larval age and the time spent in the unsuitable landscape matrix (Pechenik, 1999). Similar time-related mortality costs due to depletion of energy reserves have been assumed in aerially dispersing arthropods (Bell et al., 2005), but they are less likely in winddispersing plants like orchids in which even limited reserves inside the seeds are sufficient for survival for a year or longer (Arditti & Ghani, 2000). Water-dispersed seeds of terrestrial plants have a high chance of degenerating before reaching land or being predated by fish during transfer (Donnelly & Walters, 2008).

#### (b) Transfer costs in actively dispersing arthropods

In his seminal paper, Roff (1977) demonstrated the existence of energetic and reproductive costs of flight in *Drosophila melanogaster*. These costs were shown to decrease with body size (Roff, 1977). Further research in insects has shown that energetic investment (Berrigan, 1991; Combes & Dudley, 2009; Hedenstrom, Ellington & Wolf, 2001; Srygley, 2004; Srygley & Ellington, 1999; Srygley *et al.*, 2009) in flight or ambulatory movements decrease fecundity (Gu *et al.*, 2006; Langellotto *et al.*, 2000; Lorenz, 2007; Nespolo, Roff &

Fairbairn, 2008; Polis et al., 1998; Saglam, Roff & Fairbairn, 2008; Zera & Bottsford, 2001). Survival costs are either direct through increased predation rates (Aukema & Raffa, 2004; Galeotti & Inglisa, 2001; Korb & Linsenmair, 2002; Srygley, 2004) or deferred due to a lowered insecticide resistance (Vasquez-Castro et al., 2009). Movement is also associated with other behaviours like foraging and mate location, and it is questionable the extent to which reported costs of movement during dispersal uniquely apply to transfer as added costs, or instead are no more than baseline costs associated with such routine behaviours (Van Dyck & Baguette, 2005). The existence of true added dispersal cost associated with movement probably is a matter of the species' space-use strategy (Mueller & Fagan, 2008) and strongly phenotype dependent (Bowler & Benton, 2009). Indeed, mortality or attrition costs are likely significantly higher in species using patchy resources within a matrix of unsuitable habitat. When specific dispersal phenotypes are adapted to risky transfers, costs of investments in specific 'machinery' are likely incurred (see Section IV.2).

Transfer costs are likely to exist in insects using flight for dispersal only, or animals for which it is shown that movement distances are larger during transfer than for other movements such as those for foraging or other routine behaviours. Territorial insects with a sedentary life style would be suitable candidate species to find such effects. However, many inferences related to transfer costs have been made by comparing costs between functional winged and wingless morphs (e.g. Guerra & Pollack, 2009; Lorenz, 2007; Mole & Zera, 1994; Roff et al., 2003, 1999; Roff & DeRose, 2001; Stirling et al., 2001; Zhao & Zera, 2006), which confounds multiple costs. There is some evidence, however, that in dimorphic insects (e.g. aphids, beetles, bugs and grasshoppers) costs are predominantly paid during development, hence before the actual departure. In this sense, the study of Zera, Sall & Otto (1999) is unique. They demonstrated that female crickets (Gryllus assimilis) subjected to a substantial period of continuous tethered flight had significantly lower amounts of total lipid, triglyceride and total soluble carbohydrate compared to control females that did not fly. Long-term stimulated flights-assumed to be equivalent to genuine dispersal-consequently consumed larger amounts of lipids and carbohydrates relative to short flights (Zera et al., 1999). Recently, Gibbs et al. (2010) demonstrated that such costs may also be incurred by future generations in the speckled wood butterfly Pararge aegeria.

#### (c) Transfer costs in actively dispersing vertebrates

Similar costs have been recorded for actively dispersing vertebrates to those discussed above for actively dispersing invertebrates. Costs of (predation-related) mortality and energy loss are recorded in reptiles (Amo, Lopez & Martin, 2007; Bonnet, Guy & Shine, 1999; Clark *et al.*, 2008; Hamann, Jessop & Schauble, 2007; Jessop, Hamann & Limpus, 2004; Pietrek, Walker & Novaro, 2009; Winne & Hopkins, 2006). In fishes, however, costs are generally more associated with migration processes rather than dispersal.

In contrast to dispersal, migration also comprises movement away from the natal habitat during some life stages, but with a return to natal sites for breeding. Increased mortality is often due to increased energetic costs (Aarestrup *et al.*, 2005; Cooke *et al.*, 2006; Rand & Hinch, 1998; Rand *et al.*, 2006), or other costs related to extreme physical environments (Keefer, Peery & Heinrich, 2008), or elevated exposure to parasites (Krkosek *et al.*, 2009). Field experimental approaches have also found a reduction in fecundity with increased displacement distances (Crossin *et al.*, 2004; Jonsson & Jonsson, 2006; Kinnison *et al.*, 2001).

In birds, direct mortality risk during transfer appears to be a prominent cost (e.g. Bowman & Robel, 1977; Daniels & Walters, 2000; Hines, 1986; Kenward et al., 1999; Matthysen, 1999; Naef-Daenzer & Gruebler, 2008; Whittaker & Marzluff, 2009; Wiens et al., 2006). This mortality is often related to movement through either unfamiliar or inhospitable environments, but again empirical evidence is very scarce. Costs are sometimes humaninduced: collision with wind turbines or power lines (Real & Manosa, 2001; Smallwood, Rugge & Morrison, 2009), road kills (Massemin, Le Maho & Handrich, 1998) or human persecution (Kenward et al., 1999; Real & Manosa, 2001). There are several experimental studies demonstrating energetic costs associated with flight speed, which may lead to reduced future survival (Bowlin, Cochran & Wikelski, 2005; Johnson et al., 2006; Mandel et al., 2008; Masman & Klaassen, 1987; Pennycuick & Desanto, 1989; Schnell & Hellack, 1979; Vanderwerf, 2008; Videler, Weihs & Daan, 1983). In mammals, increased mortality costs due to road kill and predation (Boinski et al., 2005; Gillis & Krebs, 2000; Johnson et al., 2009; Klar et al., 2009) or wounding (Solomon, 2003; Soulsbury et al., 2008) are documented. Physiological costs due to increased energy expenditure during movement have also been recorded (e.g. Boldt & Ingold, 2005; Fish et al., 2001; Girard, 2001; Gustine et al., 2006; Johnson et al., 2002a, b; Rosen & Trites, 2002; Schaeffer et al., 2005).

#### (4) (Post)-settlement

The most obvious settlement costs have been recorded in plants. In the novel environment, seeds may experience massive mortality for instance by predation, fungal infections and rot (Herrera et al., 1994; Holl, 2002; Houle, 1992; Howe, 1993; Kiviniemi, 2001). Germination and seedling growth might be suppressed (Guariguata, Arias-Le Claire & Jones, 2002; Herrera et al., 1994; Holl, 2002; Lehouck et al., 2009) or seedling mortality may be increased considerably (Hughes & Westoby, 1992; Jansen, Bongers & van der Meer, 2008; Lehouck et al., 2009). While these costs are in principle levied at any distance from the maternal habitat or mother plant, seed and seedling mortality are suggested to decrease with increasing distance from the parent due to fewer natural enemies []anzen-Connell effect (Nathan & Casagrandi, 2004)]. According to the latter, assuming that habitat availability is to some degree spatially autocorrelated, the Janzen-Connell effect may occur over tens of metres

(depending on the species), but at larger distances mortality may increase through seeds arriving in less suitable habitat. Costs will therefore change in a non-linear fashion with seed dispersal distance, due to higher levels of enemies close to home, but increased costs of arriving in unsuitable habitat at greater distances. While directed dispersal through endozoochory may overcome the latter, increased densitydependent regulation through competition imposes new costs for seeds dispersed by other means than gut-passage (Spiegel & Nathan, 2010).

In passively dispersing animals survival after settlement levies probably one of strongest costs. In marine plankton, these costs are due to the active production of anchoring byssus threads (Olivier & Retiere, 2006) or silk production in terrestrial arthropods (Fingerut et al., 2009, 2006). In clams, chemicals are produced during settlement to attract conspecifics which aggregate as an anti-predator strategy (Huang, Todd & Guest, 2007). In other bivalves, settlement in crowded environments leads to density-dependent starvation among recent settlers (Olafsson et al., 1994). Social or groupliving arthropods face Allee effects when settling in habitat below carrying capacity (Aukema & Raffa, 2004; Bilde et al., 2007; Calleri, Rosengaus & Traniello, 2006). These integration costs can be of the same magnitude as costs related to settlement in low-quality sink habitat (Boughton, 1999; Itioka & Inoue, 1991; Jones & Parker, 2000; Vessby & Wiktelius, 2003) and maladaptation (Hansson et al., 2004).

Birds (Forero, Donazar & Hiraldo, 2002; Hansson et al., 2004; Nilsson, 1989; van der Jeugd, 2001; Vanderwerf, 2008), but also mammals (Cant, Otali & Mwanguhya, 2001), may lose their social rank after settlement into a novel social context and may suffer from high levels of aggression. Decreased survival (Brown, Brown & Brazeal, 2008) or reproductive success (Part, 1991) due to loss of familiarity with the environment but also due to loss of benefits from parental nepotism (Dickinson et al., 2009; Griesser & Ekman, 2004; Nystrand, 2007) are examples of opportunity costs of dispersal. Griesser & Ekman (2004) demonstrated that offspring may benefit from nepotistic antipredator behaviours through parental alarm calls in or near the natal territory only. Marr, Keller & Arcese (2002) showed clear outbreeding costs in song sparrows (Melospiza melodia) inhabiting an island system. Because these costs pass through F1 and subsequent generations through the offspring that are negatively affected, it differs from habitat mismatching, a process in which individuals settle in marginal habitat with an immediate impact on the immigrant's performance.

Finally, settlement costs are documented to depend on both the individual phenotype and the cause of dispersal. For example in the common lizard, *Lacerta vivipara*, social individuals pay higher fitness costs when they settle in lowdensity habitat (Cote, Boudsocq & Clobert, 2008; Cote & Clobert, 2007*a*). In the same species, individuals dispersing because of kin competition will take more risks (Cote & Clobert, 2010) and experience reduced fitness when they settle in an already occupied area (Le Galliard *et al.*, 2005) compared to a non-occupied one (Cote & Clobert, 2007a).

## IV. LIFE-HISTORY TRADE-OFFS AND FEEDBACKS AMONG DISPERSAL PHASES

## (1) Origin of trade-offs

Trade-offs can be under simple or pleiotropic genetic control through genetic correlations and/or epistasis. These correlations are likely to be expressed between and within dispersal-related phenotypic traits including morphological, physiological, behavioural and life-history traits. Genetic trade-offs between functional wings and insecticide resistance (Vasquez-Castro et al., 2009) or disease resistance (Adamo & Parsons, 2006; Calleri et al., 2006) are examples of deferred survival costs. Investments in flight morphology for longdistance movements reduces acceleration speed in butterflies, inducing a negative impact on male-male interactions and subsequent territory-holding ability (Berwaerts, Aerts & Van Dyck, 2006; Bonte & Van Dyck, 2009; Kemp, Wiklund & van Dyck, 2006). In crickets, winged males experience costs in secondary sexual traits, like calling performance (Roff et al., 2003). Kinnison, Unwin & Quinn (2003) experimentally showed that induced migratory costs in chinook salmon Oncorhynchus tshawytscha not only reduced energy reserves available for competition, but also decreased male investment in secondary sexual traits. Although this study dealt with migration, it nevertheless shows that costs of movement may shift the balance between natural and sexual selection and that these may induce a selection pressure on settlement abilities (see Section IV.2). Another example demonstrating trade-offs between pre-departure and settlement can be found in water striders as large-winged individuals may experience foraging costs because the large wings hamper mobility over the water surface (Goodwyn & Fujisaki, 2007).

Trade-offs can subsequently induce dispersal syndromes (or personalities in the case of correlative behaviours) with either negative or positive correlations between the different phases of the dispersal process (Sih, Bell & Johnson, 2004*a*; Sih *et al.*, 2004*b*). For example, larger dispersal distances have been observed in bold compared to shy individuals in both birds and fishes (Dingemanse *et al.*, 2003; Fraser *et al.*, 2001). In the ciliate *Tetrahymena thermophila* (Schtickzelle *et al.*, 2009) and the lizard *Uta stansburiana* (Sinervo & Clobert, 2003), a trade-off between dispersal and cooperation has been detected with dispersive phenotypes being least cooperative and/or bold.

While genetic correlations (the genotype) constrain cost reduction, we should also be aware that costs will differ in magnitude according to the phenotype. Environmentally induced dispersal costs will therefore select for phenotypedependent dispersal strategies (Clobert *et al.*, 2009). To what extent the context at different spatial scales steers quantitative changes of the observed within-individual correlations in dispersal traits (Cote & Clobert, 2007*b*) is currently unclear. In plants, germination rates and the settlement success of seedlings from small seeds may depend strongly on the local conditions that induce variation in resource availability and allocation (Coomes & Grubb, 2003), which may obscure the observation of emigration-colonisation trade-offs. Soil

nutrient conditions and intraspecific competition have been shown to influence wind dispersal in seeds because of changes in plant height and neighbouring vegetation structure (Soons & Heil, 2002; Soons et al., 2005). In general, and as repeatedly shown in birds (Ashton & Armstrong, 2002; Balbontin et al., 2009; Cam, Monnat & Hines, 2003; Ellsworth & Belthoff, 1999; Martin, Kitchens & Hines, 2007) and arthropods (Bonte, Lukac & Lens, 2008a), deterioration of local habitat conditions, including the presence of parasites (Altizer, Oberhauser & Brower, 2000; Goodacre et al., 2009), during development negatively impacts body condition. This in turn may have consequences for dispersal due to energetic constraints. As with suboptimal environmental habitat conditions, poor body condition due to inbreeding depression may equally depress departure or pre-departure investments, as has been shown in plants (Mix et al., 2006; Pico, Ouborg & Van Groenendael, 2004, 2003) and in spiders (Bonte, 2009). Environmental constraints may subsequently depress dispersal in individuals in poor condition, but because they induce a positive correlation between body condition and dispersal, they generate 'superdispersers', having both high fitness and departure capacities. When these dispersing phenotypes are more likely to settle in high-quality habitats than individuals in poor condition, so-called silver spoon effects emerge (Stamps, 2006). Such correlations are an example of a "disperser" or "colonizer syndrome" in which highly dispersive and/or mobile individuals show rapid development, early reproduction and high fecundity (Baker & Stebbins, 1965). This covariation can have a genetic basis as demonstrated in the Glanville fritillary Melitaea cinxia with butterflies bearing allele *Pgi-f* having higher mobility, fecundity and lifespan (Saastamoinen, 2007). Interestingly, flight performance of heterozygotes is higher than of homozygotes, especially at lower ambient temperatures (Niitepold et al., 2009), possibly due to kinetic superiority of the former and suggest an overdominance at Pgi (i.e. selective advantage of heterozygotes; Orsini et al., 2009). Heterozygote superiority and the species' typical metapopulation structure are therefore expected to maintain genetic variation in Pgi (Zheng, Ovaskainen & Hanski, 2009). Individuals showing such positive correlations between flight ability and other life-history traits are also called fugitive species (Hutchinson, 1951). In general, the emergence of these positively correlated strategies is explained by increased success in colonizing vacant habitat (Bonte & de la Pena, 2009; Burton et al., 2010; Dingle, Evans & Palmer, 1988; Lavie & Ritte, 1978).

## (2) Trade-offs and feedbacks among dispersal phases

While dispersal costs are generally assumed to be an intrinsic property of the entire process, it follows from our review that certain costs during the dispersal process could be more prevalent than others. As such, costs incurred at one phase may affect costs during others and can exert a selection pressure on other phases to minimize overall costs.

#### (a) Costs incurred during development and dispersal initiation

Because costs are often levied during the development or initiation phase, apparent low costs during the dispersal process may be a direct result of substantial costs that have been paid predominantly during development. The dispersal process is, however, always strongly contextdependent (e.g. landscape, social context, weather conditions) and evolved condition-dependent strategies are expected in all organisms (Clobert et al., 2009). This necessitates the evolution of a perceptual machinery (with costs taken during development) to translate the information about the environment into departure decision making (cognitive and memorizing capacities). It is unlikely that the perceptual ability has evolved specifically due to dispersal-related selection pressures but rather as a result of multi-layered selection due to e.g. foraging, mate location, and predator detection.

Pre-departure adaptations presumably involve major evolutionary transitions with higher levels of similarity among related taxa. Pre-departure costs are however not entirely genetically imprinted but may be subject to phenotypic plasticity in response to altered conditions during predeparture development (Benard & McCauley, 2008). For instance, Bicyclus anynanas butterflies can alter their body allocation in relation to the environmental conditions (food availability) experienced during development. This is turn affects their flight ability as well as costs of flight (Saastamoinen et al., 2010). Similarly, Merckx & Van Dyck (2006) showed effects of the landscape on flight morphology in the speckled wood butterfly. In a spider of crop habitats, temperature adaptively affected departure dependent on the predominant landscape context (Bonte et al., 2008b). Given the relevance of phenotypic plasticity as an adaptation to environmental heterogeneity, it is remarkable that only a few studies have specifically addressed this question for pre-departure costs. While flexibility in transfer in relation to landscape context and subsequent costs are widely acknowledged, adaptive plasticity in departure responses is expected to be especially prevalent in those taxa unable to control their dispersal trajectory (dispersal kernel). In wind-dispersing plants, plasticity as a result of environmental and genetic constraints has been recorded in relation to inbreeding (Pico et al., 2004), vegetation height (Soons & Heil, 2002) and weather (Soons & Bullock, 2008), but it remains an open question to what degree these induced changes are adaptive rather than a constraining outcome.

#### (b) Costs incurred during transfer

Selection pressures arising from mortality risk during dispersal can ultimately induce responses in departure thresholds according to the expected fitness of emigration. This has been observed in typical area-scaling immigrants with passive dispersal (e.g. ballooning spiders and plants). Spiders from small habitat islands have a lower emigration propensity at higher wind velocities compared to individuals from large, continuous habitat (Bonte *et al.*, 2007, 2006). Dispersal limitation by behavioural avoidance of crossing a habitat boundary when dispersal is costly is another example (Bonte, Lens & Maelfait, 2004; Schtickzelle & Baguette, 2003; Schtickzelle *et al.*, 2007; Schtickzelle, Mennechez & Baguette, 2006). Soons & Bullock (2008) and Jongejans *et al.* (2007) demonstrated condition-dependent (i.e. non-random) seed-release strategies. These strategies involve morphological adaptations to release seeds under specific meteorological conditions. Although costs during departure are rarely documented, similar feedbacks towards the development of sensory mechanisms might be expected.

#### (c) Costs incurred during settlement and integration

When settlement costs (i.e. failure to reach suitable habitat) are high due to low, spatially uncorrelated habitat availability, we expect an investment in the development of sensory abilities to discriminate suitable habitat in which to settle. Suitable habitat is likely recognised by innate mechanisms or by cues related to conditions in the natal habitat that induce natal habitat preference (Mabry & Stamps, 2008; Stamps & Blozis, 2006; Stamps, Krishnan & Willits, 2009; Stamps & Swaisgood, 2007). These organisms are therefore expected to switch from an areascaling settlement, in which colonisation is predominantly determined by the availability of habitat they cross during transfer, to a perimeter-scaling immigration strategy in which organisms have higher probabilities to select habitat based on the habitat's edge/surface ratio (Englund & Hamback, 2007).

The evolution of perceptual abilities has been shown in a woodland butterfly living in a patchwork of arable and forested landscape compared to conspecifics inhabiting continuous woodland landscapes (Merckx & Van Dyck, 2007). The development of mechanisms that allow settlement in suitable habitat is a so-called habitat-matching process (Edelaar, Siepielski & Clobert, 2008). This evolved sensory mechanism is a good example of trade-offs, where risk and energy costs paid during pre-departure positively feedback decreasing the settlement costs.

Changes in landscape structure might thus alter costs of dispersal and the subsequent evolution of dispersal through, for instance, changes in departure behaviour or locomotory structures. As such, evolution will be in the direction of decreasing costs of dispersal by selecting for traits that facilitate transfer (e.g. flight muscles, larger wings), facilitate settlement (i.e. perceptual abilities) or decrease dispersal rates and subsequent incurred costs. While evolutionary changes that reduce dispersal costs are likely to induce other costs (i.e. energetic costs or increased kin competition), natural selection is expected to balance both. If local conditions vary within metapopulations, such costs can lead to polymorphisms and eventually to sympatric speciation (Doebeli & Ruxton, 1997). Any absence of dispersal or excessive dispersal rates may, however, induce substantial costs through the failure of local adaptation (Billiard & Lenormand, 2005). Indeed, because dispersal is expected to

be tightly related to gene flow, philopatry will lead to the absence of gene flow and consequently decrease the genetic variation on which natural selection can act. By contrast, high levels of gene flow achieved through large dispersal distances will be responsible for gene swamping. High dispersal distances will consequently erode any local adaptations. The spatial network, specific dispersal rates and the distribution of multiple interacting species will consequently have a strong impact on patterns of local adaptation (Prugnolle et al., 2005; Vogwill, Fenton & Brockhurst, 2010) with pronounced effects on co-evolutionary processes in geographic mosaics (Barbour et al., 2009; de la Peña, D'Hondt & Bonte, 2011; King et al., 2009; Nuismer, 2006; Smith et al., 2010; Thompson, 2005). In the absence of habitat-matching strategies, costs of maladaptation are likely to be positively correlated to genetic distance between populations. Therefore, such integration costs can be expected to select against longdistance dispersal, by inducing selection pressures on specific departure behaviour or morphology. Recent studies have demonstrated such different selection pressures on long- and short-distance dispersal (Bonte, Hovestadt & Poethke, 2010b; Levin et al., 2003).

Opportunity costs due to changes in the social environment at settlement may also feedback on strategies at the departure or pre-departure phases. For instance, if costs at settlement due to increased harassment are high, selection towards body-condition-dependent strategies is expected (Gyllenberg, Kisdi & Utz, 2008). In the case of (eu)social animals (animals in which group living yields fitness benefits), severe costs would be expected when group benefits disappear, or when settlement is into a genetically different population (Griesser et al., 2008; Kahlenberg et al., 2008). In this case, selection would be expected to reduce the dispersal distance when kin structure is highly positively spatially correlated. Alternatively, emigration processes that maintain group structure such as budding or restricted dispersal by inseminated females can evolve (Kummerli et al., 2009; Lehmann & Keller, 2006). By contrast, local kin competition may induce selection pressures that increase emigration rates and dispersal distance strategies relative to non-kin environments, and alter the cost-benefit ratio expected for individual dispersers in an heterogeneous environment (Leturque & Rousset, 2002). This would subsequently generate an absence of balanced dispersal between habitats and a deviation from the species' ideal free distribution.

Opportunity costs should be considered as the ultimate trade-off in fitness prospects between philopatric and dispersive individuals, or in relation to dispersal distance. This means that benefits lost in the natal environment for a disperser are compensated through the alternative next-best option. As such, costs taken during dispersal imply that costs of staying in the natal environment are dismissed. Because of this inherent correlated cost and benefit balance between (pre-)departure and settlement, they should be considered as a cost of the entire dispersal process rather than of a separate dispersal phase. However, as argued before, we here explicitly consider them as settlement cost, and these costs are already taken when preparing transfer to new habitat.

#### V. CHANGING COSTS IN A CHANGING WORLD

Rapid environmental changes in land-use and climate (Smith et al., 2009) are likely to influence the costs of dispersal. In general, increasing habitat fragmentation induces non-linearity in dispersal evolution, with at the start a clear evolution towards high dispersal rates followed by a bifurcation and the evolution of both residential and dispersive strategies, and eventually a clear counter-selection against dispersal if habitat fragmentation becomes severe (Heino & Hanski, 2001; Mathias, Kisdi & Olivieri, 2001). While increasing habitat fragmentation will decrease the connectedness of suitable habitat and resources and as such increase transfer costs, rapid climate change is expected to induce changes in life histories such as the duration of juvenile stages during which dispersal occurs (Berg et al., 2010; O'Connor et al., 2007). Changes in phenology together with changes in weather conditions are additionally likely to change the temporal windows of dispersal and may eventually impact connectivity. Indeed, movement costs are related to ambient temperature or wind velocity, but changes in climate may also affect dispersal trajectories in marine systems due to changes in oceanic currents (Parmesan, 2006). Species can adapt to global warming by phenotypic plasticity in thermal responses or by genetic adaptations (Pulido & Berthold, 2004), but non-adaptive plasticity due to changes in individual body condition may provoke substantial changes in dispersal costs.

Passively dispersing organisms appear to experience predominantly pre-departure and settlement costs in fragmented landscapes with limited habitat availability. By contrast, other species have developed sensory mechanisms to reduce these costs, and have higher settlement probabilities. The selection pressure due to landscape changes can therefore be expected to differ between these two groups, and we expect evolutionary changes in dispersal to become prevalent in the latter group. Plants, and probably passively dispersing invertebrates, are not able to develop any of these sensory-motor adaptations. Increased costs due to habitat fragmentation will then inevitably lead to decreasing dispersal rates, eventually leading to evolutionary traps (Schlaepfer, Runge & Sherman, 2002) or evolutionary suicide in cases where reduced dispersal induced strong fitness costs due to, for instance, inbreeding depression (Colas et al., 1997). Fig. 3 shows a schematic (and purely hypothetical) representation of how trade-offs may induce failures of connectivity restoration. The main idea is that adaptation towards reduced dispersal is possible during the process of habitat fragmentation (Massot, Clobert & Ferriere, 2008), but that the accompanied loss of standing genetic variation hampers evolution in the opposite direction when connectivity is restored.



Fig. 3. A schematic representation of how trade-offs among costs may give rise to different genotypes of a hypothetical insect under a scenario of habitat loss and fragmentation and how restoration success may consequently fail. The insects are drawn according to the allocated investments in dispersal (wing size and thorax size), perceptual ability (eye size) and fecundity (abdomen size). The bar diagram depicts the hypothetical energy allocation to fecundity (blue), perceptual ability (red) and dispersal ability (green). In an intact landscape (A; the reference), costs of dispersal are low and perceptual abilities are only moderately developed. As a consequence, inhabiting genotypes allocate relatively more energy to fecundity than to wing development and perceptual ability. After sudden habitat loss and subsequent fragmentation, high selection pressures will give rise to either highly mobile genotypes with well-developed perceptual abilities (B1) or genotypes with a loss of dispersal (B2). In the former case (B1), costs on fecundity are high but the species is able to occupy all patches in a panmictic population. In the latter case (B2), the species will become philopatric and residential at the local carrying capacity in the four subpopulations. After restoration efforts to decrease dispersal mortality by creating stepping stones, loss of genetic variation and low selection pressures will impede fast evolution, and the combined action of environmental and demographic stochasticity will remain high, thereby maintaining the population at low fecundity (C1). In the isolated subpopulations (C2), stepping stones will not be colonised and inbreeding may subsequently induce a decrease in fecundity.

Global warming is expected to cause deeply modified dispersal both at the northern and southern margins of a species' distribution by favouring individuals with specific syndromes that maximise fitness at range margins. For example, large cane toads *Bufo marinus* (Phillips *et al.*,

2008) and aggressive mountain bluebirds Sialia currucoides (Duckworth & Badyaev, 2007) are favoured at their invasion front due to the combined effects of enhanced transfer efficiency, reproduction or territory occupation. On the other hand, trade-offs between dispersal and other traits that enhance adaptation to novel habitats may constrain range expansion. In the common lizard, for instance, individuals with lower levels of melanin in their back skin are more resistant to environmental conditions at the range margin, but also have reduced dispersal (Lepetz et al., 2009). This short-term adaptation acts as an evolutionary trap since an enhanced dispersal should be necessary in the long term to escape deleterious effects of warming (Massot et al., 2008). Evolutionary traps due to evolved investments are also prevalent when directed dispersal has evolved in response to large frugivores that have become extinct in recent times. Here, costs are taken by plants during development, i.e. through the production of conspicuous structures (often arilles or fleshy fruit pulp) containing the seeds, but benefits during transfer and settlement have disappeared, leading to deterministic extinction, as for instance observed in some long-lived tropical trees (Guimaraes, Galetti & Jordano, 2008). At expanding range margins reduced costs of settlement (more space, no preoccupation) has selected for increased pre-departure costs in, for instance, cane toads (Phillips et al., 2008) and insects (Leotard et al., 2009; Thomas et al., 2001) due to investment in longer legs, and longer wings or earlier reproduction, respectively.

Finally, costs incurred at the other phases of dispersal should be considered for connectivity restoration, translocation and reintroduction programs (i.e. assisted migration), which are designed to decrease transfer costs, but do not consider potentially high integration costs. While forced dispersal may be costly, we do however stress from a scientific point-of-view that costs taken during forced dispersal are not informative on the prevalence of costs during natural dispersal and care should be taken when using this approach in experimental studies.

## VI. IMPLICATIONS FOR MODELLING

Whilst many models have been developed to investigate the causes and consequences of different dispersal strategies, costs have been incorporated in very simplistic ways. The vast majority of models have focussed on establishing the evolutionarily stable rate of emigration (e.g. Hovestadt, Messner & Poethke, 2001; Poethke, Hovestadt & Mitesser, 2003; Rousset & Gandon, 2002), and have typically assumed that emigrating individuals suffer a constant probability of mortality (that is explicitly or implicitly assumed to occur during transfer). In most cases these models have considered density-independent probabilities of departure, although the evolution of density-dependent emigration strategies has been addressed by several recent studies (Poethke & Hovestadt, 2002; Travis *et al.*, 2009). But very few studies have explored the evolution of movement or settlement strategies (e.g., Ruxton & Rohani, 1998; Heino & Hanski, 2001; Matthias *et al.*, 2001; Barton *et al.*, 2009). Due to the rather narrow focus on the departure phase, there has been hardly any theoretical consideration on the causes or consequences of different dispersal cost structures (but see J.M.J. Travis, in preparation). Doing so will emphasise both the need to decompose the costs and provide a model structure within which the partitioning of costs is straightforward to achieve.

Substantial recent progress has been made in modelling the movement of both plants and animals and there is a clear opportunity to utilise these approaches in modelling the transfer phase of dispersal. For plants, there is a suite of mechanistic models simulating the movements of seeds by wind (for reviews see Kuparinen, 2006 and Nathan et al., 2011). Animal movement through heterogeneous landscapes can now be modelled using, for example, biased correlated random walks (Barton et al., 2009) or Ornstein-Uhlenbeck processes (Smouse et al., 2010). By using these process-based models it is possible to ask how the movement behaviour of an individual during the transfer phase influences the time that it takes to locate a suitable habitat patch, or the predation risk it suffers during dispersal (Delgado et al., 2010; Zollner & Lima, 2005). In an evolutionary context, we can ask how selection is expected to shape the movement rules in response to a particular environmental context. Initial work in this direction has demonstrated that we should typically expect highly correlated inter-patch movement of dispersing individuals (Heinz & Strand, 2006). It has been suggested that individuals should engage in riskier movement behaviours when the landscape matrix is less hostile (Barton et al., 2009). More complex spatial environments can be modelled by incorporating matrix elements with different associated energetic costs of movement or different risks of predation; an individual's ability to move through the matrix, or to perceive a habitat patch (or to locate better quality matrix), may depend upon pre-departure investment in potentially costly visual or olfactory apparatus. Models could usefully be deployed to ask how investment in perceptual ability might depend upon the quality and spatial structure of the habitat and landscape matrix.

A dispersing animal that reaches a potential habitat patch has to decide whether or not to settle at that site or to search for another site, and thus, return to the transient dispersal phase. Remarkably few models explicitly incorporate settlement decisions or the evolution of settlement behaviour. One possible rule is that individuals deterministically decline to settle in a patch if their expected reproductive success in that patch is below a threshold and continue searching until they locate a patch where the expected fitness exceeds this constant threshold (Ruxton & Rohani, 1998). In reality, individuals will expend energy and time as they search for and assess the quality of habitat patches, and these costs are likely to mean that the settlement threshold will change. An individual will become increasingly likely to accept lower quality habitat over time. Hence, we expect an individual to have a higher probability of accepting lower quality habitat (e.g. more crowded habitat) when the cost of moving through the matrix is higher.

The new generation of spatial simulation models also needs to incorporate other issues highlighted herein, including trade-offs such as between dispersal ability and reproduction. Surprisingly few models have explored the evolution of dispersal where increased movement ability comes at a cost to other key life-history traits such as fecundity (see King & Roff, 2010; Burton et al., 2010 for exceptions) or where costs of dispersal evolve (Billiard & Lenormand, 2005). King & Roff (2010) have presented the results of a model where flight dimorphic insects trade-off fecundity for dispersal ability. In this model only the macropterous individuals disperse, but the probability that a macropterous individual emigrates depends upon the amount of resources it has devoted to flight ability. As the majority of the models exploring dispersal evolution, the model applies a survival cost to dispersal that is assumed to integrate different potential costs associated with emigrating, including the energetic costs of flight. It is also typical of much of the theoretical literature in assuming that emigrating individuals enter into a common migrant pool, and surviving migrants are distributed randomly amongst patches. By integrating life-history trade-off approaches similar to those described by King & Roff (2010) in models allowing for the evolution of more complex inter-patch movement behaviours (e.g. Heinz & Strand, 2006; Barton et al., 2009) it would be possible to develop a flexible modelling framework much better suited to addressing many of the interesting questions that arise as we decompose the dispersal process, and its associated costs, into different phases.

#### VII. CONCLUSIONS

(1) Costs are ubiquitous at different phases of the dispersal process. While costs of transfer have been widely documented in actively dispersing organisms as well as costs of departure in passively dispersing organisms, our review emphasises that costs are levied during all dispersal phases. We still lack insights as to what degree special dispersal behaviours are associated with different costs in comparison with dispersal through more routine behaviours. Prospecting costs during dispersal preparation are likely to be ubiquitous in actively dispersing organisms, but are understudied. Quantification of these costs by careful experiments should be the next phase of research.

(2) Because costs during each of the dispersal phases are expected to induce trade-offs with traits relevant to other phases, different correlated responses are expected in relation to the specific social and environmental context.

(3) Within populations, trade-offs among traits at the individual level may give rise to heterogeneity of alternative strategies in different environmental or social contexts. Among populations, these observed correlated responses may be conserved, but also reversed, depending on the balance between resource acquisition and allocation.

(4) Because costs are balanced by environmental properties and individual condition, trade-offs will induce

condition- and context-dependent dispersal strategies. We should therefore abandon the idea that dispersal is a simple, fixed process and acknowledge the existence of complex spatial and temporal patterns in dispersal.

(5) Ultimately, cost-partitioning mechanisms are expected to exert selection pressure on pre-dispersal (developmental) investments in either mobility or sensory mechanisms. Costs may alternatively induce selection at settlement, for instance to improve habitat matching rather than non-selective settlement.

(6) From a conservation point of view, costs of dispersal are not only incurred during transfer but also during earlier life phases and during settlement. Understanding such costs is essential within the context of introductions, assisted dispersal (which phenotypes to select, presence of costs due to habitat matching and local adaptation) and the restoration of landscape connectedness (effectiveness of corridors according to altered movement rules, migration load etc.).

(7) Depending on settlement costs, animals in particular may use apparently more costly transfer routes in order to decrease costs at settlement. It is therefore highly relevant that both theoretical approaches and applied conservation modelling approaches should consider the existence of multiple costs, and trade-offs among them, to understand adaptive dispersal responses of organisms in landscapes subject to global change.

(8) Whereas there is growing interest by modellers in how costs at the distinguished dispersal phases may shape the evolution of dispersal genotypes, the recognition and understanding of the multiple cost structures is equally relevant in applied ecological questions.

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#### **IX. REFERENCES**

AARESTRUP, K., JEPSEN, N., KOED, A. & PEDERSEN, S. (2005). Movement and mortality of stocked brown trout in a stream. *Journal of Fish Biology* 66, 721–728.

ADAMO, S. A. & PARSONS, N. M. (2006). The emergency life-history stage and immunity in the cricket, *Gryllus texensis. Animal Behaviour* 72, 235–244. AGREN, J. & SCHEMSKE, D. W. (1993). Outcrossing rate and inbreeding depression in 2 annual monoecious herbs, *Begonia hirsuta* and *B. semiovata*. *Evolution* **47**, 125–135.

- AHLROTH, P., ALATALO, R. V., HYVARINEN, E. & SUHONEN, J. (1999). Geographical variation in wing polymorphism of the waterstrider Aquarius najas (Heteroptera, Gerridae). Journal of Evolutionary Biology 12, 156–160.
- ALLEN, J. D. & MCALISTER, J. S. (2007). Testing rates of planktonic versus benthic predation in the field. *Journal of Experimental Marine Biology and Ecology* 347, 77–87.
- ALTIZER, S. M., OBERHAUSER, K. S. & BROWER, L. P. (2000). Associations between host migration and the prevalence of a protozoan parasite in natural populations of adult monarch butterflies. *Ecological Entomology* 25, 125–139.
- AMO, L., LOPEZ, P. & MARTIN, J. (2007). Habitat deterioration affects body condition of lizards: A behavioral approach with *Iberolacerta cyreni* lizards inhabiting ski resorts. *Biological Conservation* 135, 77–85.
- ARDITTI, J. & GHANI, A. K. A. (2000). Tansley review No. 110 Numerical and physical properties of orchid seeds and their biological implications. *New Phytologist* 145, 367–421.
- ASHTON, J. C. & ARMSTRONG, D. P. (2002). Facultative prioritization of wing growth in the Welcome Swallow *Hirundo neozena*. *Ibis* 144, 470–477.
- AUKEMA, B. H. & RAFFA, K. F. (2004). Does aggregation benefit bark beetles by diluting predation? Links between a group-colonisation strategy and the absence of emergent multiple predator effects. *Ecological Entomology* 29, 129–138.
- BAGUETTE, M. & VAN DYCK, H. (2007). Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landscape Ecology* 22, 1117–1129.
- BAKER, H. G. & STEBBINS, G. L. (1965). *The Genetics of Colonising Species*. Academic Press, New York.
- BALBONTIN, J., MOLLER, A. P., HERMOSELL, I. G., MARZAL, A., REVIRIEGO, M. & DE LOPE, F. (2009). Geographic patterns of natal dispersal in barn swallows *Hirundo nustica* from Denmark and Spain. *Behavioral Ecology and Sociobiology* 63, 1197–1205.
- BARBOUR, R. C., O'REILLY-WAPSTRA, J. M., DE LITTLE, D. W., JORDAN, G. J., STEANE, D. A., HUMPHREYS, J. R., BAILEY, J. K., WHITHAM, T. G. & POTTS, B. M. (2009). A geographic mosaic of genetic variation within a foundation tree species and its community-level consequences. *Ecology* **90**, 1762–1772.
- BARTON, K. A., PHILLIPS, B. L., MORALES, J. M. & TRAVIS, J. M. J. (2009). The evolution of an 'intelligent' dispersal strategy: biased, correlated random walks in patchy landscapes. *Oikos* 118, 309–319.
- BELICHON, S., CLOBERT, J. & MASSOT, M. (1996). Are there differences in fitness components between philopatric and dispersing individuals? *Acta Oecologica-International Journal of Ecology* 17, 503–517.
- BELL, J. R., BOHAN, D. A., SHAW, E. M. & WEYMAN, G. S. (2005). Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research* 95, 69–114.
- BENARD, M. F. & MCCAULEY, S. J. (2008). Integrating across life-history stages: Consequences of natal habitat effects on dispersal. *American Naturalist* 171, 553–567.
- BENNETT, C. E. & MARSHALL, D. J. (2005). The relative energetic costs of the larval period, larval swimming and metamorphosis for the ascidian *Diplosoma listerianum*. *Marine and Freshwater Behaviour and Physiology* 38, 21–29.
- BERG, M. P., KIERS, E. T., DRIESSEN, G., VAN DER HEIJDEN, M., KOOI, B. W., KUENEN, F., LIEFTING, M., VERHOEF, H. A. & ELLERS, J. (2010). Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology* 16, 587–598.
- BERRIGAN, D. (1991). Lift production in the Flesh Fly, Neobellieria (= Sarcophaga) bullata Parker. Functional Ecology 5, 448–456.
- BERRIGAN, D. & LIGHTON, J. R. B. (1994). Energetics of pedestrian locomotion in adult male blowflies, *Protophormia terraenovae* (Diptera, Calliphoridae). *Physiological Zoology* 67, 1140–1153.
- BERWAERTS, K., AERTS, P. & VAN DYCK, H. (2006). On the sex-specific mechanisms of butterfly flight: flight performance relative to flight morphology, wing kinematics, and sex in *Pararge aegeria. Biological Journal of the Linnean Society* 89, 675–687.
- BILDE, T., COATES, K. S., BIRKHOFER, K., BIRD, T., MAKLAKOV, A. A., LUBIN, Y. & AVILES, L. (2007). Survival benefits select for group living in a social spider despite reproductive costs. *Journal of Evolutionary Biology* 20, 2412–2426.
- BILLIARD, S. & LENORMAND, T. (2005). Evolution of migration under kin selection and local adaptation. *Evolution* 59, 13–23.
- BIRKEMOE, T. & LEINAAS, H. P. (1999). Reproductive biology of the arctic collembolan Hypogastrura tullbergi. *Ecography* 22, 31–39.
- BLACKLEDGE, T. A. & GILLESPIE, R. G. (2004). Convergent evolution of behavior in an adaptive radiation of Hawaiian web-building spiders. *Proceedings of the National Academy of Sciences of the United States of America* 101, 16228–16233.
- BLANCKENHORN, W. U. (1994). Fitness consequences of alternative life-histories in water-striders, Aquarius remigis (Heteroptera, Gerridae). Oecologia 97, 354–365.
- BLATE, G. M., PEART, D. R. & LEIGHTON, M. (1998). Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian rainforest. *Oikos* 82, 522–538.

- BLONDEL, J., DIAS, P. C., MAISTRE, M. & PERRET, P. (1993). Habitat heterogeneity and life-history variation of mediterranean blue tits (*Parus caeruleus*). Auk 110, 511–520.
- BOINSKI, S., KAUFFMAN, L., EHMKE, E., SCHET, S. & VREEDZAAM, A. (2005). Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii, S. boliviensis and S. sciureus*): I. Divergent costs and benefits. *Behaviour* 142, 525–632.
- BOLDT, A. & INGOLD, P. (2005). Effects of air traffic, snow cover and weather on altitudinal short-term and medium-term movements of female Alpine chamois *Rupicapra rupicapra* in winter. *Wildlife Biology* 11, 351–362.
- BONNET, X., GUY, N. & SHINE, R. (1999). The dangers of leaving home: dispersal and mortality in snakes. *Biological conservation* 89, 39–50.
- BONTE, D. (2009). Inbreeding depresses short and long distance dispersal in three congeneric spiders. *Journal of Evolutionary Biology* 22, 1429–1434.
- BONTE, D., BOSSUYT, B. & LENS, L. (2007). Aerial dispersal plasticity under different wind velocities in a salt marsh wolf spider. *Behavioral Ecology* 18, 438–443.
- BONTE, D. & DE LA PENA, E. (2009). Evolution of body condition-dependent dispersal in metapopulations. *Journal of Evolutionary Biology* 22, 1242–1251.
- BONTE, D., DE ROISSART, A., VANDEGEHUCHTE, M. L., BALLHORN, D. J., VAN LEEUWEN, T. & DE LA PENA, E. (2010*a*). Local adaptation of aboveground herbivores towards plant phenotypes induced by soil biota. *Plos One* 5: e11174.
- BONTE, D., HOVESTADT, T. & POETHKE, H. J. (2010b). Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. Oikos 119, 560–566.
- BONTE, D., LENS, L. & MAELFAIT, J. P. (2004). Lack of homeward orientation and increased mobility result in high emigration rates from low-quality fragments in a dune wolf spider. *Journal of Animal Ecology* 73, 643–650.
- BONTE, D., LUKAC, M. & LENS, L. (2008a). Starvation affects pre-dispersal behaviour of Erigone spiders. Basic and Applied Ecology 9, 308–315.
- BONTE, D., TRAVIS, J. M. J., DE CLERCQ, N., ZWERTVAEGHER, I. & LENS, L. (2008b). Thermal conditions during juvenile development affect adult dispersal in a spider. Proceedings of the National Academy of Sciences of the United States of America 105, 17000–17005.
- BONTE, D. & VAN DYCK, H. (2009). Mate-locating behaviour, habitat-use, and flight morphology relative to rainforest disturbance in an Afrotropical butterfly. *Biological Journal of the Linnean Society* 96, 830–839.
- BONTE, D., VANDEN BORRE, J., LENS, L. & MAELFAIT, J. P. (2006). Geographical variation in wolf spider dispersal behaviour is related to landscape structure. *Animal Behaviour* 72, 655–662.
- BONTE, D., VANDENBROECKE, N., LENS, L. & MAELFAIT, J.-P. (2003). Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. *Proc. Roy. Soc. London B* 270, 1601–1607.
- BOUGHTON, D. A. (1999). Empirical evidence for complex source-sink dynamics with alternative states in a butterfly metapopulation. *Ecology* 80, 2727–2739.
- BOWLER, D. E. & BENTON, T. G. (2009). Variation in dispersal mortality and dispersal propensity among individuals: the effects of age, sex and resource availability. *Journal* of Animal Ecology 78, 1234–1241.
- BOWLIN, M. S., COCHRAN, W. W. & WIKELSKI, M. C. (2005). Biotelemetry of New World thrushes during migration: Physiology, energetics and orientation in the wild. *Integrative and Comparative Biology* 45, 295–304.
- BOWMAN, T. J. & ROBEL, R. J. (1977). Brood Break-up, Dispersal, Mobility, and Mortality of Juvenile Prairie Chickens. *Journal of Wildlife Management* 41, 27–34.
- BROWN, C. R., BROWN, M. B. & BRAZEAL, K. R. (2008). Familiarity with breeding habitat improves daily survival in colonial cliff swallows. *Animal Behaviour* 76, 1201–1210.
- BURT, A. (1995). Perspective the evolution of fitness. Evolution 49, 1-8.
- BURTON, O.J., PHILLIPS, B. L. & TRAVIS, J. M. J. (2010). Trade-offs and the evolution of life-histories during range expansion. *Ecology Letters* 13, 1210–1220.
- BUSCH, J. W. (2005). Inbreeding depression in self-incompatible and self-compatible populations of Leavenworthia alabamica. *Heredity* 94, 159–165.
- CALLERI, D. V., ROSENGAUS, R. B. & TRANIELLO, J. F. A. (2006). Disease and colony establishment in the dampwood termite *Zootermopsis angusticollis*: survival and fitness consequences of infection in primary reproductives. *Insectes Sociaux* 53, 204–211.
- CAM, E., MONNAT, J. Y. & HINES, J. E. (2003). Long-term fitness consequences of early conditions in the kittiwake. *Journal of Animal Ecology* 72, 411–424.
- CANETE, J. I., GALLARDO, C. S., ROMERO, M. & AMBLER, R. (2007). Planktonic drifting dispersal of early juvenile *Trochita calyptraeaformis* Born 1778 [Gastropoda : Calyptraeidae]. *Journal of Experimental Marine Biology and Ecology* 346, 1–7.
- CANT, M. A., OTALI, E. & MWANGUHYA, F. (2001). Eviction and dispersal in cooperatively breeding banded mongooses (*Mungos mungo*). *Journal of Zoology (London*)254, 155–162.
- CARROLL, S. P., HENDRY, A. P., REZNICK, D. N. & FOX, C. W. (2007). Evolution on ecological time-scales. *Functional Ecology* 21, 387–393.
- CHAVES, O. M. & AVALOS, G. (2006). Is the inverse leafing phenology of the dry forest understory shrub *Jacquinia nervosa* (Theophrastaceae) a strategy to escape herbivory? *Revista De Biologia Tropical* 54, 951–963.
- CHEPTOU, P. O., CARRUE, O., ROUIFED, S. & CANTAREL, A. (2008). Rapid evolution of seed dispersal in an urban environment in the weed Crepis sancta. *Proceedings of* the National Academy of Sciences of the United States of America 105, 3796–3799.

- CHEUNG, S. G., LUK, K. C. & SHIN, P. K. S. (2006). Predator-Labeling Effect on Byssus Production in Marine Mussels *Perna viridis* (L.) and *Brachidontes variabilis* (Krauss). *Journal of Chemical Ecology* 32, 1501–1512.
- CHRISTENSEN, K. M. & WHITHAM, T. G. (1991). Indirect herbivore mediation of avian seed dispersal in pinyon pine. *Ecology* 72, 534–542.
- CHRISTIANINI, A. V. & OLIVEIRA, P. S. (2010). Birds and ants provide complementary seed dispersal in a neotropical savanna. *Journal of Ecology* 98, 573-582.
- CLARK, R. W., BROWN, W. S., STECHERT, R. & ZAMUDIO, K. R. (2008). Integrating individual behavior and landscape genetics: the population structure of timber rattlesnake hibernacula. *Molecular Ecology* 17, 719–730.
- CLOBERT, J., LE GALLIARD, J. F., COTE, J., MEYLAN, S. & MASSOT, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* 12, 197–209.
- COCHRANE, E. P. (2003). The need to be eaten: Balanites wilsoniana with and without elephant seed-dispersal. Journal of Tropical Ecology 19, 579–589.
- COLAS, B., OLIVIERI, I. & RIBA, M. (1997). Centaurea corymbosa, a cliff-dwelling species tottering on the brink of extinction: A demographic and genetic study. Proceedings of the National Academy of Sciences of the United States of America 94, 3471–3476.
- COMBES, S. A. & DUDLEY, R. (2009). Turbulence-driven instabilities limit insect flight performance. Proceedings of the National Academy of Sciences of the United States of America 106, 9105–9108.
- CONWAY, H. E. & KRING, T. J. (2004). Wing formation and reproduction from insecticide-treated cotton aphids (Homoptera : Aphididae). *Journal of Entomological Science* 39, 407–416.
- COOKE, S. J., HINCH, S. G., CROSSIN, G. T., PATTERSON, D. A., ENGLISH, K. K., HEALEY, M. C., SHRIMPTON, J. M., VAN DER KRAAK, G. & FARRELL, A. P. (2006). Mechanistic basis of individual mortality in pacific salmon during spawning migrations. *Ecology* 87, 1575–1586.
- COOMES, D. A. & GRUBB, P. J. (2003). Colonization, tolerance, competition and seedsize variation within functional groups. *Trends in Ecology & Evolution* 18, 283–291.
- COSYNS, E., DELPORTE, A., LENS, L. & HOFFMANN, M. (2005). Germination success of temperate grassland species after passage through ungulate and rabbit guts. *J. Ecology* 93, 393–361.
- COTE, J., BOUDSOCQ, S. & CLOBERT, J. (2008). Density, social information, and space use in the common lizard (*Laceta vivipara*). *Behavioral Ecology* **19**, 163–168.
- COTE, J. & CLOBERT, J. (2007a). Social information and emigration: lessons from immigrants. *Ecology Letters* 10, 411–417.
- COTE, J. & CLOBERT, J. (2007b). Social personalities influence natal dispersal in a lizard. Proceedings of the Royal Society B-Biological Sciences 274, 383–390.
- COTE, J. & CLOBERT, J. (2010). Risky dispersal: avoiding kin competition despite uncertainty. *Ecology* 91, 1485–1493.
- CRAIG, C. L. (1997). Evolution of arthropod silks. Annu. Rev. Entomol. 42, 231-267.
- CRAWFORD, D. W. (1992). Metabolic cost of motility in planktonic protists theoretical considerations on size scaling and swimming speed. *Microbial Ecology* 24, 1–10.
- CRESSMAN, R. & KRIVAN, V. (2006). Migration dynamics for the ideal free distribution. *American Naturalist* 168, 384–397.
- CRNOKRAK, P. & ROFF, D. A. (1995). Fitness differences associated with calling behaviour in the two wing morphs of male sand crickets, *Gryllus firmus. Animal Behaviour* 50, 1475–1481.
- CRNOKRAK, P. & ROFF, D. A. (1998a). The contingency of fitness: an analysis of food restriction on the macroptery-reproduction trade-off in crickets. *Animal Behaviour* 56, 433–441.
- CRNOKRAK, P. & ROFF, D. A. (1998b). The genetic basis of the trade-off between calling and wing morph in males of the cricket *Gryllus firmus. Evolution* 52, 1111–1118.
- CRNOKRAK, P. & ROFF, D. A. (2000). The trade-off to macroptery in the cricket Gryllus firmus: a path analysis in males. Journal of Evolutionary Biology 13, 396–408.
- CROSSIN, G. T., HINCH, S. G., FARRELL, A. P., HIGGS, D. A., LOTTO, A. G., OAKES, J. D. & HEALEY, M. C. (2004). Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. *Journal of Fish Biology* 65, 788–810.
- CUMMINGS, V. J., PRIDMORE, R. D., THRUSH, S. F. & HEWITT, J. E. (1993). Emergence and floating behaviors of postsettlement juveniles of *Macomona liliana* (bivalvia, tellinacea). *Marine Behaviour and Physiology* 24, 25–32.
- DANIELS, S. J. & WALTERS, J. R. (2000). Between-year breeding dispersal in Redcockaded Woodpeckers: Multiple causes and estimated cost. *Ecology* 81, 2473–2484.
- DAVIS, R. W. & WEIHS, D. (2007). Locomotion in diving elephant seals: physical and physiological constraints. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 362, 2141–2150.
- DE LA PEÑA, E., D'HONDT, B. & BONTE, D. (2011). Landscape structure, dispersal and the evolution of antagonistic plant-herbivore interactions. *Ecography* **34**, 480–487.
- DEBLOK, J. W. & TANMAAS, M. (1977). Function of byssus threads in young postlarval mytilus. *Nature* 267, 558–558.
- DELGADO, M. D., PENTERIANI, V., REVILLA, E. & NAMS, V. O. (2010). The effect of phenotypic traits and external cues on natal dispersal movements. *Journal of Animal Ecology* 79, 620–632.

- DEL MAR DELGADO, M., RATIKAINEN, I. I. & KOKKO, H. (2011). Inertia: the discrepancy between individual and common good in dispersal and prospecting behaviour. *Biological Reviews*. doi: 10.1111/j.1469-185X.2010.00167.x
- DENNO, R. F., DOUGLASS, L. W. & JACOBS, D. (1985). Crowding and host plant nutrition - environmental determinants of wing-form in *Prokelisia marginata*. *Ecology* 66, 1588–1596.
- DERR, J. A., ALDEN, B. & DINGLE, H. (1981). Insect life histories in relation to migration, body size, and host plant array - a comparative-study of Dysdercus. *Journal of Animal Ecology* 50, 181–193.
- D'HONDT, B., BOSSUYT, B., HOFFMANN, M. & BONTE, D. (2008). Dung beetles as secondary seed dispersers in a temperate grassland. *Basic and Applied Ecology* 9, 542–549.
- DICKINSON, J. L., EUAPARADORN, M., GREENWALD, K., MITRA, C. & SHIZUKA, D. (2009). Cooperation and competition: nepotistic tolerance and intrasexual aggression in western bluebird winter groups. *Animal Behaviour* **77**, 867–872.
- DINGEMANSE, N. J., BOTH, C., VAN NOORDWIJK, A. J., RUTTEN, A. L. & DRENT, P. J. (2003). Natal dispersal and personalities in great tits (*Parus major*). Proceedings of the Royal Society of London Series B-Biological Sciences 270, 741–747.
- DINGLE, H. (1996). Migration: the biology of life on the move. Oxford University Press, New York.
- DINGLE, H., BLAKLEY, N. R. & MILLER, E. R. (1980). Variation in body size and flight performance in milkweed bugs (Oncopeltus). *Evolution* **34**, 371–385.
- DINGLE, H., EVANS, K. E. & PALMER, J. O. (1988). Responses to selection among life-history traits in a nonmigratory population of milkweed bugs (*Oncopellus fasciatus*). *Evolution* 42, 79–92.
- DIXON, A. F. G., HORTH, S. & KINDLMANN, P. (1993). Migration in insects Cost and strategies. *Journal of Animal Ecology* 62, 182–190.
- DIXON, A. F. G. & KINDLMANN, P. (1999). Cost of flight apparatus and optimum body size of aphid migrants. *Ecology* 80, 1678–1690.
- DOEBELI, M. & RUXTON, G. D. (1997). Evolution of dispersal rates in metapopulation models: Branching and cyclic dynamics in phenotype space. *Evolution* 51, 1730–1741.
- DONNELLY, M. J. & WALTERS, L. J. (2008). Water and boating activity as dispersal vectors for *Schinus terebinthifolius* (Brazilian pepper) seeds in freshwater and estuarine habitats. *Estuaries and Coasts* **31**, 960–968.
- DUCKWORTH, R. A. & BADYAEV, A. V. (2007). Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 15017–15022.
- DUNCAN, F. D. & CREWE, R. M. (1993). A comparison of the energetics of foraging of 3 species of *Leptogenys* (Hymenoptera, Formicidae). *Physiological Entomology* 18, 372–378.
- EDELAAR, P., SIEPIELSKI, A. M. & CLOBERT, J. (2008). Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. *Evolution* 62, 2462–2472.
- EDWARDS, G. R. & CRAWLEY, M. J. (1999). Rodent seed predation and seedling recruitment in mesic grassland. *Oecologia* 118, 288–296.
- ELLSWORTH, E. A. & BELTHOFF, J. R. (1999). Effects of social status on the dispersal behaviour of juvenile western screech-owls. *Animal Behaviour* 57, 883–892.
- ENGLUND, G. & HAMBACK, P. A. (2007). Scale dependence of immigration rates: models, metrics and data. *Journal of Animal Ecology* 76, 30–35.
- EPP, R. W. & LEWIS, W. M. (1984). Cost and speed of locomotion for rotifers. *Oecologia* 61, 289–292.
- FARNSWORTH, E. J. & ELLISON, A. M. (1997). Global patterns of pre-dispersal propagule predation in mangrove forests. *Biotropica* 29, 318–330.
- FEDRIANI, J. M. & MANZANEDA, A. J. (2005). Pre- and postdispersal seed predation by rodents: balance of food and safety. *Behavioral Ecology* **16**, 1018–1024.
- FINGERUT, J., SCHAMEL, L., FAUGNO, A., MESTRINARO, M. & HABDAS, P. (2009). Role of silk threads in the dispersal of larvae through stream pools. *Journal of Zoology* 279, 137–143.
- FINGERUT, J. T., HART, D. D. & MCNAIR, J. N. (2006). Silk filaments enhance the settlement of stream insect larvae. *Oecologia* 150, 202–212.
- FISH, F. E., FRAPPELL, P. B., BAUDINETTE, R. V. & MACFARLANE, P. M. (2001). Energetics of terrestrial locomotion of the platypus Ornithorhynchus anatinus. Journal of Experimental Biology 204, 797–803.
- FJERDINGSTAD, E. J., SCHTICKZELLE, N., MANHES, P., GUTIERREZ, A. & CLOBERT, J. (2007). Evolution of dispersal and life history strategies - Tetrahymena ciliates. *Bmc Evolutionary Biology* 7.
- FORERO, M. G., DONAZAR, J. A. & HIRALDO, F. (2002). Causes and fitness consequences of natal dispersal in a population of black kites. *Ecology* 83, 858–872.
- FORGET, P. M. (1992). Regeneration ecology of *Eperua grandiflora* (caesalpiniaceae), a large-seeded tree in French-Guiana. *Biotropica* 24, 146–156.
- FORSMAN, E. D., ANTHONY, R. G., REID, J. A., LOSCHL, P. J., SOVERN, S. G., TAYLOR, M., BISWELL, B. L., ELLINGSON, A., MESLOW, E. C., MILLER, G. S., SWINDLE, K. A., THRAILKILL, J. A., WAGNER, F. F. & SEAMAN, D. E. (2002). Natal and breeding dispersal of northern spotted owls. *Wildlife Monographs* 149, 1–35.
- FRASER, D. F., GILLIAM, J. F., DALEY, M. J., LE, A. N. & SKALSKI, G. T. (2001). Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. *American Naturalist* **158**, 124–135.

- FRESNILLO, B. & EHLERS, B. K. (2008). Variation in dispersability among mainland and island populations of three wind dispersed plant species. *Plant Systematics and Evolution* 270, 243–255.
- FRIEDENBERG, N. A. (2003). Experimental evolution of dispersal in spatiotemporally variable microcosms. *Ecology Letters* 6, 953–959.
- FULL, R. J. & TULLIS, A. (1990). Capacity for sustained terrestrial locomotion in an insect - Energetics, thermal-dependence, and kinematics. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 160, 573–581.
- GALEOTTI, P. & INGLISA, M. (2001). Estimating predation impact on honeybees Apis mellifera L. by European bee-caters Merops apiaster L. Revue d' Ecologie: la terre et la vie 56, 373–388.
- GANDON, S. (1999). Kin competition, the cost of inbreeding and the evolution of dispersal. *Journal of Theoretical Biology* 200, 345–364.
- GANDON, S. & MICHALAKIS, Y. (1999). Evolutionarily stable dispersal rate in a metapopulation with extinctions and kin competition. *Journal of Theoretical Biology* 199, 275–290.
- GARCIA, D., GOMEZ, J. M., ZAMORA, R. & HODAR, J. A. (2000). Do empty *Juniperus communis* seeds defend filled seeds against predation by *Apodemus sylvaticus? Ecoscience* 7, 214–221.
- GAVRILETS, S., LI, H. & VOSE, M. D. (2000). Patterns of parapatric speciation. Evolution 54, 1126–1134.
- GIBBS, M., BREUKER, C. J., HESKETH, H., HAILS, R. S. & VAN DYCK, H. (2010). Maternal effects, flight versus fecundity trade-offs, and offspring immune defence in the Speckled Wood butterfly, *Pararge aegeria. Bmc Evolutionary Biology* **10**, 10.
- GILLIS, E. A. & KREBS, C. J. (2000). Survival of dispersing versus philopatric juvenile snowshoe hares: Do dispersers die? *Oikos* 90, 343–346.
- GIRARD, I. (2001). Field cost of activity in the kit fox, Vulpes macrotis. Physiological and Biochemical Zoology 74, 191–202.
- GOODACRE, S. L., MARTIN, O. Y., BONTE, D., HUTCHINGS, L., WOOLLEY, C., IBRAHIM, K., THOMAS, C. F. G. & HEWITT, G. M. (2009). Microbial modification of host long-distance dispersal capacity. *Bmc Biology* 7:32.
- GOODWYN, P. P. & FUJISAKI, K. (2007). Sexual conflicts, loss of flight, and fitness gains in locomotion of polymorphic water striders. *Entomologia Experimentalis Et Applicata* 124, 249–259.
- GREEN, P. T. & JUNIPER, P. A. (2004). Seed mass, seedling herbivory and the reserve effect in tropical rainforest seedlings. *Functional Ecology* 18, 539–547.
- GREIG, N. (1993). Predispersal seed predation on 5 piper species in tropical rain-forest. *Oecologia* 93, 412–420.
- GRIESSER, M. & EKMAN, A. (2004). Nepotistic alarm calling in the Siberian jay, Perisoreus infaustus. Animal Behaviour 67, 933–939.
- GRIESSER, M., NYSTRAND, M., EGGERS, S. & EKMAN, J. (2008). Social constraints limit dispersal and settlement decisions in a group-living bird species. *Behavioral Ecology* 19, 317–324.
- GRIMM, C. (1995). Seed predators and the fruiting phenology of *Pithecellobium pallens* (leguminosae) in thornscrub, north-eastern Mexico. *Journal of Tropical Ecology* 11, 321–332.
- GU, H. N. & DANTHANARAYANA, W. (1992). Quantitative genetic analysis of dispersal in *Epiphyas postvittana*. 2. Genetic covariations between flight capacity and life-history traits. *Heredity* 68, 61–69.
- GU, H. N., HUGHES, J. & DORN, S. (2006). Trade-off between mobility and fitness in Cydia pomonella L. (Lepidoptera : Tortricidae). Ecological Entomology 31, 68–74.
- GUARIGUATA, M. R., ARIAS-LE CLAIRE, H. & JONES, G. (2002). Tree seed fate in a logged and fragmented forest landscape, northeastern Costa Rica. *Biotropica* 34, 405–415.
- GUERRA, R. F. & ADES, C. (2002). An analysis of travel costs on transport of load and nest building in golden hamster. *Behavioural Processes* 57, 7–28.
- GUERRA, P. A. & POLLACK, G. S. (2009). Flight behaviour attenuates the trade-off between flight capability and reproduction in a wing polymorphic cricket. *Biology Letters* 5, 229–231.
- GUIMARAES, P. R., GALETTI, M. & JORDANO, P. (2008). Seed Dispersal Anachronisms: Rethinking the Fruits Extinct Megafauna Ate. Plos One 3, 13.
- GUSTINE, D. D., PARKER, K. L., LAY, R. J., GILLINGHAM, M. P. & HEARD, D. C. (2006). Interpreting resource selection at different scales for woodland caribou in winter. *Journal of Wildlife Management* **70**, 1601–1614.
- GYLLENBERG, M., KISDI, E. & UTZ, M. (2008). Evolution of condition-dependent dispersal under kin competition. *Journal of Mathematical Biology* 57, 285–307.
- HALL, A. R. & COLEGRAVE, N. (2008). Decay of unused characters by selection and drift. *Journal of Evolutionary Biology* 21, 610–617.
- HAMANN, M., JESSOP, T. S. & SCHAUBLE, C. S. (2007). Fuel use and corticosterone dynamics in hatchling green sea turtles (*Chelonia mydas*) during natal dispersal. *Journal* of Experimental Marine Biology and Ecology 353, 13–21.
- HANSKI, I., ERALAHTI, C., KANKARE, M., OVASKAINEN, O. & SIREN, H. (2004). Variation in migration propensity among individuals maintained by landscape structure. *Ecology Letters* 7, 958–966.
- HANSSON, B., BENSCH, S. & HASSELQUIST, D. (2004). Lifetime fitness of short- and long-distance dispersing great reed warblers. *Evolution* 58, 2546–2557.

- HEDENSTROM, A., ELLINGTON, C. P. & WOLF, T. J. (2001). Wing wear, aerodynamics and flight energetics in bumblebees (*Bombus terrestris*): an experimental study. *Functional Ecology* 15, 417–422.
- HEIDINGER, I. M. M., POETHKE, H. J., BONTE, D. & HEIN, S. (2009). The effect of translocation on movement behaviour-A test of the assumptions of behavioural studies. *Behavioural Processes* 82, 12–17.
- HEIN, S., GOMBERT, J., HOVESTADT, T. & POETHKE, H. J. (2003). Movement patterns of the bush cricket *Platycleis albopunctata* in different types of habitat: matrix is not always matrix. *Ecological Entomology* 28, 432–438.
- HEINO, M. & HANSKI, I. (2001). Evolution of migration rate in a spatially realistic metapopulation model. *American Naturalist* 157, 495–511.
- HEINZ, S. K. & STRAND, E. (2006). Adaptive patch searching strategies in fragmented landscapes. *Evolutionary Ecology* 20, 113–130.
- HENDRY, A. P., NOSIL, P. & RIESEBERG, L. H. (2007). The speed of ecological speciation. *Functional Ecology* 21, 455–464.
- HENDRY, A. P. & TAYLOR, E. B. (2004). How much of the variation in adaptive divergence can be explained by gene flow? - An evaluation using lake-stream stickleback pairs. *Evolution* 58, 2319–2331.
- HEREFORD, J. (2009). A quantitative survey of local adaptation and fitness trade-offs. *American Naturalist* 173, 579–588.
- HERRERA, C. M., JORDANO, P., LOPEZSORIA, L. & AMAT, J. A. (1994). Recruitment of a mast-fruiting, bird-dispersed tree - bridging frugivore activity and seedling establishment. *Ecological Monographs* **64**, 315–344.
- HIDDINK, J. G., KOCK, R. P. & WOLFF, W. J. (2002). Active pelagic migrations of the bivalve Macoma balthica are dangerous. *Marine Biology* 140, 1149–1156.
- HIDDINK, J. G. & WOLFF, W. J. (2002). Changes in distribution and decrease in numbers during migration of the bivalve *Macoma balthica*. *Marine Ecology-Progress Series* 233, 117–130.
- HINES, J. E. (1986). Survival and reproduction of dispersing Blue Grouse. Condor 88, 43–49.
- HINSLEY, S. A. (2000). The costs of multiple patch use by birds. Landscape Ecology 15, 765–775.
- HOLL, K. D. (2002). Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. *Journal of Ecology* 90, 179–187.
- HORVATH, T. G. & LAMBERTI, G. A. (1999). Mortality of zebra mussel, Dreissena polymorpha, veligers during downstream transport. Freshwater Biology 42, 69–76.
- HOSHIZAKI, K., SUZUKI, W. & SASAKI, S. (1997). Impacts of secondary seed dispersal and herbivory on seedling survival in *Aesculus turbinata*. *Journal of Vegetation Science* 8, 735–742.
- HOULE, G. (1992). Spatial relationship between seed and seedling abundance and mortality in a deciduous forest of north-eastern North-America. *Journal of Ecology* 80, 99–108.
- HOVESTADT, T., MESSNER, S. & POETHKE, H. J. (2001). Evolution of reduced dispersal mortality and 'fat-tailed' dispersal kernels in autocorrelated landscapes. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268, 385–391.
- HOWE, H. F. (1993). Aspects of variation in a neotropical seed dispersal system. Vegetatio 108, 149–162.
- HU, X. S. & LI, B. L. (2003). On migration load of seeds and pollen grains in a local population. *Heredity* **90**, 162–168.
- HUANG, D. W., TODD, P. A. & GUEST, J. R. (2007). Movement and aggregation in the fluted giant clam (*Tridacna squamosa L.*). *Journal of Experimental Marine Biology and Ecology* 342, 269–281.
- HUBERTY, A. F. & DENNO, R. F. (2006). Trade-off in investment between dispersal and ingestion capability in phytophagous insects and its ecological implications. *Oecologia* 148, 226–234.
- HUGHES, L. & WESTOBY, M. (1992). Fate of seeds adapted for dispersal by ants in Australian sclerophyll vegetation. *Ecology* 73, 1285–1299.
- HUTCHINSON, G. E. (1951). Copepodology for the ornithologist. *Ecology* **32**, 571–577. ITIOKA, T. & INOUE, T. (1991). Settling-site selection and survival of 2 scale insects,
- Ceroplastes rubens and C. ceriferus, on citrus trees. Researches on Population Ecology 33, 69-85.
- JANSEN, P. A., BONGERS, F. & VAN DER MEER, P. J. (2008). Is farther seed dispersal better? Spatial patterns of offspring mortality in three rainforest tree species with different dispersal abilities. *Ecography* 31, 43–52.
- JESSOP, T. S., HAMANN, M. & LIMPUS, C. J. (2004). Body condition and physiological changes in male green turtles during breeding. *Marine Ecology-Progress Series* 276, 281–288.
- JOHNSON, C. A., FRYXELL, J. M., THOMPSON, I. D. & BAKER, J. A. (2009). Mortality risk increases with natal dispersal distance in American martens. *Proceedings of the Royal Society Biological Sciences Series B* 276, 3361–3367.
- JOHNSON, C. G. (1963). Physiological factors in insect migration by flight. Nature 198, 423–427.
- JOHNSON, C. J., PARKER, K. L., HEARD, D. C. & GILLINGHAM, M. P. (2002a). A multiscale behavioral approach to understanding the movements of woodland caribou. *Ecological Applications* 12, 1840–1860.
- JOHNSON, C. J., PARKER, K. L., HEARD, D. C. & GILLINGHAM, M. P. (2002b). Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology* **71**, 225–235.

- JOHNSON, M. D., SHERRY, T. W., HOLMES, R. T. & MARRA, P. P. (2006). Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. *Conservation Biology* 20, 1433–1444.
- JONES, T. C. & PARKER, P. G. (2000). Costs and benefits of foraging associated with delayed dispersal in the spider Anelosimus studiosus (Araneae, Theridiidae). Journal of Arachnology 28, 61–69.
- JONGEJANS, E., PEDATELLA, N. M., SHEA, K., SKARPAAS, O. & AUHL, R. (2007). Seed release by invasive thistles: the impact of plant and environmental factors. *Proceedings of the Royal Society B-Biological Sciences* 274, 2457–2464.
- JONSSON, B. & JONSSON, N. (2006). Life-history effects of migratory costs in anadromous brown trout. *Journal of Fish Biology* 69, 860–869.
- KAHLENBERG, S. M., THOMPSON, M. E., MULLER, M. N. & WRANGHAM, R. W. (2008). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour* 76, 1497–1509.
- KARLSSON, B. & JOHANSSON, A. (2008). Seasonal polyphenism and developmental trade-offs between flight ability and egg laying in a pierid butterfly. *Proceedings of the Royal Society B-Biological Sciences* 275, 2131–2136.
- KEEFER, M. L., PEERY, C. A. & HEINRICH, M. J. (2008). Temperature-mediated en route migration mortality and travel rates of endangered Snake River sockeye salmon. *Ecology of Freshwater Fish* 17, 136–145.
- KEITH, D. & PELLOW, B. (2005). Effects of Javan rusa deer (*Cervus timorensis*) on native plant species in the Jibbon-Bundeena Area, Royal National Park, New South Wales. *Proceedings of the Linnean Society of New South Wales* 126, 99–110.
- KEMP, D. J., WIKLUND, C. & VAN DYCK, H. (2006). Contest behaviour in the speckled wood butterfly (*Pararge aegeria*): seasonal phenotypic plasticity and the functional significance of flight performance. *Behavioral Ecology and Sociobiology* 59, 403–411.
- KENWARD, R. E., MARCSTROM, V. & KARLBOM, M. (1999). Demographic estimates from radio-tagging: models of age-specific survival and breeding in the goshawk. *Journal of Animal Ecology* 68, 1020–1033.
- KING, E. G. & ROFF, D. A. (2010). Modeling the evolution of phenotypic plasticity in resource allocation in wing-dimorphic insects. *American Naturalist* 175, 702–716.
- KING, K. C., DELPH, L. F., JOKELA, J. & LIVELY, C. M. (2009). The geographic mosaic of sex and the red queen. *Current Biology* 19, 1438–1441.
- KINNISON, M. T., UNWIN, M. J., HENDRY, A. P. & QUINN, T. P. (2001). Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. *Evolution* 55, 1656–1667.
- KINNISON, M. T., UNWIN, M. J. & QUINN, T. P. (2003). Migratory costs and contemporary evolution of reproductive allocation in male chinook salmon. *Journal* of Evolutionary Biology 16, 1257–1269.
- KISIMOTO, R. (1956). Effect of crowding during the larval period on the determination of the wing-form of an adult planthopper. *Nature* 178, 641–642.
- KIVINIEMI, K. (2001). Evolution of recruitment features in plants: a comparative study of species in the Rosaceae. *Oikos* 94, 250–262.
- KLAR, N., HERRMANN, M. & KRAMER-SCHADT, S. (2009). Effects and mitigation of road impacts on individual movement behavior of wildcats. *Journal of Wildlife Management* 73, 631–638.
- Кокко, H. & LOPEZ-SEPULCRE, A. (2006). From individual dispersal to species ranges: perspectives for a changing world. *Science* 313, 789–791.
- KORB, J. & LINSENMAIR, K. E. (2002). Evaluation of predation risk in the collectively foraging termite *Macrotermes bellicosus*. *Insectes Sociaux* 49, 264–269.
- KRAM, R. (1996). Inexpensive load carrying by rhinoceros beetles. *Journal of Experimental Biology* 199, 609-612.
- KRAMER, D. L. & MCLAUGHLIN, R. L. (2001). The behavioral ecology of intermittent locomotion. American Zoologist 41, 137–153.
- KRIVAN, V., CRESSMAN, R. & SCHNEIDER, C. (2008). The ideal free distribution: A review and synthesis of the game-theoretic perspective. *Theoretical Population Biology* 73, 403–425.
- KRKOSEK, M., MORTON, A., VOLPE, J. P. & LEWIS, M. A. (2009). Sea lice and salmon population dynamics: effects of exposure time for migratory fish. *Proceedings of the Royal Society B-Biological Sciences* 276, 2819–2828.
- KUMMERLI, R., GARDNER, A., WEST, S. A. & GRIFFIN, A. S. (2009). Limited dispersal, budding dispersal, and cooperation: an experimental study. *Evolution* 63, 939–949.
- KUPARINEN, Å. (2006). Mechanistic models for wind dispersal. *Trends in Plant Science* 11, 296–301.
- LACHANCE, M. A. (2004). Here and there or everywhere? Bioscience 54, 884-884.
- LANGELLOTTO, G. A., DENNO, R. F. & OTT, J. R. (2000). A trade-off between flight capability and reproduction in males of a wing-dimorphic insect. *Ecology* 81, 865–875.
- LARSEN, K. W. & BOUTIN, S. (1994). Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. *Ecology* 75, 214–223.
- LAVIE, B. & RITTE, U. (1978). The relation between dispersal behaviour and reproductive fitness in the flour beetle *Tribolium castaneum*. *Canadian Journal of Genetics* and Cytology 20, 589–595.
- LECOMTE, J., BOUDJEMADI, K., SARRAZIN, F., CALLY, K. & CLOBERT, J. (2004). Connectivity and homogenisation of population sizes: an experimental approach in *Lacerta vivipara. Journal of Animal Ecology* 73, 179–189.

- Le GALLIARD, J. F., FITZE, P. S., COTE, J., MASSOT, M. & CLOBERT, J. (2005). Female common lizards (*Lacerta vivipara*) do not adjust their sex-biased investment in relation to the adult sex ratio. *Journal of Evolutionary Biology* **18**, 1455–1463.
- LEHMANN, L. & KELLER, L. (2006). The evolution of cooperation and altruism a general framework and a classification of models. *Journal of Evolutionary Biology* 19, 1365–1376.
- LEHOUCK, V., SPANHOVE, T., GONSAMO, A., CORDEIRO, N. & LENS, L. (2009). Spatial and temporal effects on recruitment of an Afromontane forest tree in a threatened fragmented ecosystem. *Biological Conservation* 142, 518–528.
- LEIMU, R. & FISCHER, M. (2008). A Meta-Analysis of Local Adaptation in Plants. *Plos One* **3**.
- LEOTARD, G., DEBOUT, G., DALECKY, A., GUILLOT, S., GAUME, L., MCKEY, D. & KJELLBERG, F. (2009). Range expansion drives dispersal evolution in an equatorial three-species symbiosis. *Plos One* 4, 11.
- LEPETZ, V., MASSOT, M., CHAINE, A. & CLOBERT J. (2009). Climate warming and the evolution of morphotypes in a reptile. *Global Change Biology* 15, 454–466.
- LETURQUE, H. & ROUSSET, F. (2002). Dispersal, kin competition, and the ideal free distribution in a spatially heterogeneous population. *Theoretical Population Biology* 62, 169–180.
- LEVIN, S. A., MULLER-LANDAU, H. C., NATHAN, R. & CHAVE, J. (2003). The ecology and evolution of seed dispersal: A theoretical perspective. *Annual Review of Ecology Evolution and Systematics* 34, 575–604.
- LIGHTON, J. R. B., WEIER, J. A. & FEENER, D. H. (1993). The energetics of locomotion and load carriage in the desert harvester ant *Pogonomyrmex rugosus*. *Journal of Experimental Biology* 181, 49–61.
- LOPEZ, L. & TERBORGH, J. (2007). Seed predation and seedling herbivory as factors in tree recruitment failure on predator-free forested islands. *Journal of Tropical Ecology* 23, 129–137.
- LORENZ, M. W. (2007). Oogenesis-flight syndrome in crickets: Age-dependent egg production, flight performance, and biochemical composition of the flight muscles in adult female *Gryllus binaculatus. Journal of Insect Physiology* 53, 819–832.
- LUNDQUIST, C. J., PILDITCH, C. A. & CUMMINGS, V. J. (2004). Behaviour controls post-settlement dispersal by the juvenile bivalves Austrovenus stutchburyi and Macomona liliana. Journal of Experimental Marine Biology and Ecology 306, 51-74.
- MABRY, K. E. & STAMPS, J. A. (2008). Dispersing brush mice prefer habitat like home. Proceedings of the Royal Society B-Biological Sciences 275, 543–548.
- MANDEL, J. T., BILDSTEIN, K. L., BOHRER, G. & WINKLER, D. W. (2008). Movement ecology of migration in turkey vultures. *Proceedings of the National Academy of Sciences of the United States of America* 105, 19102–19107.
- MARDEN, J. H. & CHAI, P. (1991). Aerial predation and butterfly design How palatability, mimicry, and the need for evasive flight constrain, mass allocation. *American Naturalist* 138, 15–36.
- MARR, A. B., KELLER, L. F. & ARCESE, P. (2002). Heterosis and outbreeding depression in descendants of natural immigrants to an inbred population of song sparrows (*Melospiza melodia*). *Evolution* 56, 131–142.
- MARSHALL, D. J., PECHENIK, J. A. & KEOUGH, M. J. (2003). Larval activity levels and delayed metamorphosis affect post-larval performance in the colonial, ascidian *Diplosoma listerianum. Marine Ecology-Progress Series* 246, 153–162.
- MARTIN, J., KITCHENS, W. M. & HINES, J. E. (2007). Natal location influences movement and survival of a spatially structured population of snail kites. *Oecologia* 153, 291–301.
- MASMAN, D. & KLAASSEN, M. (1987). Energy-expenditure during free flight in trained and free-living eurasian kestrels (*Falco timunculus*). Auk **104**, 603–616.
- MASSEMIN, S., LE MAHO, Y. & HANDRICH, Y. (1998). Seasonal pattern in age, sex and body condition of barn owls *Tyto alba* killed on motorways. *Ibis* 140, 70–75.
- MASSOT, M., CLOBERT, J. & FERRIERE, R. (2008). Climate warming, dispersal inhibition and extinction risk. *Global Change Biology* 14, 461–469.
- MATHIAS, A., KISDI, E. & OLIVIERI, I. (2001). Divergent evolution of dispersal in a heterogeneous landscape. *Evolution* 55, 246–259.
- MATSUO, Y. (2006). Cost of prolonged diapause and its relationship to body size in a seed predator. *Functional Ecology* 20, 300–306.
- MATTHYSEN, E. (1999). Nuthatches (Sitta europaea: Aves) in forest fragments: demography of a patchy population. Oecologia 119, 501–509.
- MCCONAUGHA, J. R. (1992). Decapod larvae dispersal, mortality, and ecology a working hypothesis. *American Zoologist* 32, 512–523.
- MCHENRY, M. J. & PATEK, S. N. (2004). The evolution of larval morphology and swimming performance in Ascidians. *Evolution* 58, 1209–1224.
- MCKINNEY, S. T. & TOMBACK, D. F. (2007). The influence of white pine blister rust on seed dispersal in whitebark pine. *Canadian Journal of Forest Research-Revue Canadienne* De Recherche Forestiere **37**, 1044–1057.
- MERCKX, T. & VAN DYCK, H. (2006). Landscape structure and phenotypic plasticity in flight morphology in the butterfly Pararge aegeria. Oikos 113, 226–232.
- MERCKX, T. & VAN DYCK, H. (2007). Habitat fragmentation affects habitat-finding ability of the speckled wood butterfly, *Pararge aegeria* L. Animal Behaviour 74, 1029–1037.
- MILNER, R. N. C., BOOKSMYTHE, I., JENNIONS, M. D. & BACKWELL, P. R. Y. (2010). The battle of the sexes? Territory acquisition and defence in male and female fiddler crabs. *Animal Behaviour* 79, 735–738.

- MIX, C., PICO, F. X., VAN GROENENDAEL, J. M. & OUBORG, N. J. (2006). Inbreeding and soil conditions affect dispersal and components of performance of two plant species in fragmented landscapes. *Basic and Applied Ecology* 7, 59–69.
- MOLE, S. & ZERA, A. J. (1994). Differential resource consumption obviates a potential flight fecundity trade-off in the sand cricket (*Gryllus firmus*). *Functional Ecology* 8, 573–580.
- MUELLER, T. & FAGAN, W. F. (2008). Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos* 117, 654–664.
- MUSOLIN, D. L. & NUMATA, H. (2004). Late-season induction of diapause in *Nezara viridula* and its effect on adult coloration and post-diapause reproductive performance. *Entomologia Experimentalis Et Applicata* 111, 1–6.
- NAEF-DAENZER, B. & GRUEBLER, M. U. (2008). Post-fledging range use of Great Tit Parus major families in relation to chick body condition. Ardea 96, 181–190.
- NATHAN, R. & CASAGRANDI, R. (2004). A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen-Connell and beyond. *Journal of Ecology* 92, 733–746.
- NATHAN, R., KATUL, G. G., BOHRER, G., KUPARINEN, A., SOONS, M. B., THOMP-SON, S. E., TRAKHTENBROT, A. & HORN, H. S. (2011). Mechanistic models of seed dispersal by wind. *Theoretical Ecology* 4, 113–132.
- NESPOLO, R. F., ROFF, D. A. & FAIRBAIRN, D. J. (2008). Energetic trade-off between maintenance costs and flight capacity in the sand cricket (*Gryllus firmus*). Functional Ecology 22, 624–631.
- NIITEPOLD, K., SMITH, A. D., OSBORNE, J. L., REYNOLDS, D. R., CARRECK, N. L., MARTIN, A. P., MARDEN, J. H., OVASKAINEN, O. & HANSKI, I. (2009). Flight metabolic rate and Pgi genotype influence butterfly dispersal rate in the field. *Ecology* **90**, 2223–2232.
- NILSSON, J. A. (1989). Causes and consequences of natal dispersal in the marsh tit, Parus palustris. Journal of Animal Ecology 58, 619–636.
- NORAMBUENA, H. & PIPER, G. L. (2000). Impact of Apion ulicis Forster on Ulex europaeus L. seed dispersal. Biological Control 17, 267–271.
- NOVOTNY, V. (1995). Adaptive significance of wing dimorphism in males of Nilaparvata lugens. Entomologia Experimentalis et Applicata 76, 233–239.
- NUISMER, S. L. (2006). Parasite local adaptation in a geographic mosaic. *Evolution* 60, 24–30.
- NYSTRAND, M. (2007). Associating with kin affects the trade-off between energy intake and exposure to predators in a social bird species. *Animal Behaviour* 74, 497–506.
- NYSTRAND, O. & GRANSTROM, A. (2000). Predation on *Pinus sylvestris* seeds and juvenile seedlings in Swedish boreal forest in relation to stand disturbance by logging. *Journal of Applied Ecology* 37, 449–463.
- O'CONNOR, M. I., BRUNO, J. F., GAINES, S. D., HALPERN, B. S., LESTER, S. E., KINLAN, B. P. & WEISS, J. M. (2007). Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of* the National Academy of Sciences of the United States of America 104, 1266–1271.
- OLAFSSON, E. B., PETERSON, C. H. & AMBROSE, W. G. (1994). Does recruitment limitation structure populations and communities of macroinvertebrates in marine soft sediments - the relative significance of presettlement and postsettlement processes. *Oceanography and Marine Biology* **32**, 65–109.
- OLIVIER, F. & RETIERE, C. (2006). How to leave or stay on the substratum when you can't swim? Evidence of the role of mucus thread secretion by postlarvae of *Peetinaria koreni* (Malmgren) in still water and flume experiments. *Aquatic Ecology* **40**, 503–519.
- ORSINI, L., WHEAT, C. W., HAAG, C. R., KVIST, J., FRILANDER, M. J. & HANSKI, I. (2009). Fitness differences associated with Pgi SNP genotypes in the Glanville fritillary butterfly (Melitaea cinxia). *Journal of Evolutionary Biology* **22**, 367–375.
- OSTERGARD, H., HAMBACK, P. A. & EHRLEN, J. (2007). Pre-dispersal seed predation: The role of fruit abortion and selective oviposition. *Ecology* **88**, 2959–2965.
- PALMQVIST, E., LUNDBERG, P. & JONZEN, N. (2000). Linking resource matching and dispersal. *Evolutionary Ecology* 14, 1–12.
- PARMESAN, C. (2006). Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37, 637–669.
- PART, T. (1991). Philopatry pays a comparison between Collared flycatcher sisters. *American Naturalist* **138**, 790–796.
- PART, T. (1995). The importance of local familiarity and search costs for age-biased and sex-biased philopatry in the Collared Flycatcher. *Animal Behaviour* 49, 1029–1038.
- PECHENIK, J. A. (1999). On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Ecology-Progress Series* 177, 269–297.
- PECHENIK, J. A. & CERULLI, T. R. (1991). Influence of delayed metamorphosis on survival, growth, and reproduction of the marine *polychaete capitella*. *Journal of Experimental Marine Biology and Ecology* **151**, 17–27.
- PENNYCUICK, C. J. & DESANTO, T. (1989). Flight speeds and energy-requirements for White Ibises on foraging flights. Auk 106, 141–144.
- PHILLIPS, B. L., BROWN, G. P., TRAVIS, J. M. J. & SHINE, R. (2008). Reid's paradox revisited: The evolution of dispersal kernels during range expansion. *American Naturalist* **172**, 34–48.
- PICO, F. X., OUBORG, N. J. & VAN GROENENDAEL, J. M. (2003). Fitness traits and dispersal ability in the herb *Tragopogon pratensis* (Asteraceae): Decoupling the role of inbreeding depression and maternal effects. *Plant Biology* 5, 522–530.

- PICO, F. X., OUBORG, N. J. & VAN GROENENDAEL, J. (2004). Influence of selfing and maternal effects on life-cycle traits and dispersal ability in the herb *Hypochaeris radicata* (Asteraccae). *Botanical Journal of the Linnean Society* 146, 163–170.
- PIETREK, A. G., WALKER, R. S. & NOVARO, A. J. (2009). Susceptibility of lizards to predation under two levels of vegetative cover. *Journal of Arid Environments* 73, 574–577.
- POETHKE, H. J. & HOVESTADT, T. (2002). Evolution of density- and patch-sizedependent dispersal rates. Proc. R. Soc. London 269, 637-645.
- POETHKE, H. J., HOVESTADT, T. & MITESSER, O. (2003). Local extinction and the evolution of dispersal rates: causes and correlations. *The American Naturalist* 161, 631–640.
- POLIS, G. A., BARNES, J. D., SEELY, M. K., HENSCHEL, J. R. & ENDERS, M. M. (1998). Predation as a major cost of reproduction in Namib desert tenebrionid beetles. *Ecology* **79**, 2560–2566.
- PONTZER, H. (2007). Effective limb length and the scaling of locomotor cost in terrestrial animals. *Journal of Experimental Biology* **210**, 1752–1761.
- PRUGNOLLE, F., THERON, A., POINTIER, J. P., JABBOUR-ZAHAB, R., JARNE, P., DURAND, P. & DE MEEUS, T. (2005). Dispersal in a parasitic worm and its two hosts: Consequence for local adaptation. *Evolution* 59, 296–303.
- PULIDO, F. & BERTHOLD, P. (2004). Microevolutionary response to climatic change. In Birds and Climate Change, vol. 35. Advances in Ecological Research (eds A. P. MOLLER, W. FIELDER and P. BERTHOLD), pp. 151–183. Academic Press Ltd, London.
- PYWELL, R. F., BULLOCK, J. M., TALLOWIN, J. B., WALKER, K. J., WARMAN, E. A. & MASTERS, G. (2007). Enhancing diversity of species-poor grasslands: an experimental assessment of multiple constraints. *Journal of Applied Ecology* 44, 81–94.
- RAMETTE, A. & TIEDJE, J. M. (2007). Biogeography: An emerging cornerstone for understanding prokaryotic diversity, ecology, and evolution. *Microbial Ecology* 53, 197–207.
- RAND, P. S. & HINCH, S. G. (1998). Swim speeds and energy use of upriver-migrating sockeye salmon (Oncorhynchus nerka): simulating metabolic power and assessing risk of energy depletion. Canadian Journal of Fisheries and Aquatic Sciences 55, 1832–1841.
- RAND, P. S., HINCH, S. G., MORRISON, J., FOREMAN, M. G. G., MACNUTT, M. J., MACDONALD, J. S., HEALEY, M. C., FARRELL, A. P. & HIGGS, D. A. (2006). Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. *Transactions of the American Fisheries Society* 135, 655–667.
- RASANEN, K. & HENDRY, A. P. (2008). Disentangling interactions between adaptive divergence and gene flow when ecology drives diversification. *Ecology Letters* 11, 624–636.
- REAL, J. & MANOSA, S. (2001). Dispersal of juvenile and immature Bonelli's Eagles in northeastern Spain. *Journal of Raptor Research* 35, 9–14.
- RIBA, M., MAYOL, M., GILES, B. E., RONCE, O., IMBERT, E., VAN DER VELDE, M., CHAUVET, S., ERICSON, L., BIJLSMA, R., VOSMAN, B., SMULDERS, M. J. M. & OLIVIERI, I. (2009). Darwin's wind hypothesis: does it work for plant dispersal in fragmented habitats? *New Phytologist* 183, 667–677.
- ROFF, D. (1977). Dispersal in Dipterans: its costs and consequences. *J. Anim. Ecol* 46, 443–456.
- ROFF, D. A., CRNOKRAK, P. & FAIRBAIRN, D. J. (2003). The evolution of trade-offs: geographic variation in call duration and flight ability in the sand cricket, *Gryllus firmus*. *Journal of Evolutionary Biology* 16, 744–753.
- ROFF, D. A. & DEROSE, M. A. (2001). The evolution of trade-offs: Effects of inbreeding on fecundity relationships in the cricket *Gryllus firmus. Evolution* 55, 111–121.
- ROFF, D. A., MOSTOWY, S. & FAIRBAIRN, D. J. (2002). The evolution of trade-offs: Testing predictions on response to selection and environmental variation. *Evolution* 56, 84–95.
- ROFF, D. A., TUCKER, J., STIRLING, G. & FAIRBAIRN, D. J. (1999). The evolution of threshold traits: effects of selection on fecundity and correlated response in wing dimorphism in the sand cricket. *Journal of Evolutionary Biology* 12, 535–546.
- RONCE, O. (2007). How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annual Review of Ecology Evolution and Systematics 38, 231–253.
- ROSEN, D. A. S. & TRITES, A. W. (2002). Cost of transport in Steller sea lions, Eumetopias jubatus. Marine Mammal Science 18, 513–524.
- ROUSSET, F. & GANDON, S. (2002). Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. *J. Evol. Biol.* 15, 515–523.
- RUXTON, G. D. & ROHANI, P. (1998). Population floors and the persistence of chaos in ecological models. *Theoretical Population Biology* 53, 175–183.
- SAASTAMOINEN, M. (2007). Life-history, genotypic, and environmental correlates of clutch size in the Glanville fritillary butterfly. *Ecological Entomology* 32, 235–242.
- SAASTAMOINEN, M., VAN DER STERREN, D., VASTENHOUT, N., ZWAAN, B. J. & BRAKEFIELD, P. M. (2010). Predictive adaptive responses: condition-dependent impact of adult nutrition and flight in the tropical butterfly *Bicyclus anynana. American Naturalist* **176**, 686–698.
- SACK, C. & STERN, D. L. (2007). Sex and death in the male pea aphid, Acyrthosiphon pisum: The life-history effects of a wing dimorphism. Journal of Insect Science 7.
- SAGLAM, I. K., ROFF, D. A. & FAIRBAIRN, D. J. (2008). Male sand crickets tradeoff flight capability for reproductive potential. *Journal of Evolutionary Biology* 21, 997–1004.

SANFORD, E. & KELLY, M. W. (2010). Local Adaptation in Marine Invertebrates. Annual Review of Marine Science 3, 509-535.

- SCHAEFFER, P. J., VILLARIN, J. J., PIEROTTI, D. J., KELLY, D. P. & LINDSTEDT, S. L. (2005). Cost of transport is increased after cold exposure in *Monodelphis domestica*: training for inefficiency. *Journal of Experimental Biology* **208**, 3159–3167.
- SCHLAEPFER, M. A., RUNGE, M. C. & SHERMAN, P. W. (2002). Ecological and evolutionary traps. *Trends in Ecology & Evolution* 17, 474–480.
- SCHNELL, G. D. & HELLACK, J. J. (1979). Bird flight speeds in nature optimized or a compromise. American Naturalist 113, 53–66.
- SCHTICKZELLE, N. & BAGUETTE, M. (2003). Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. *Journal of Animal Ecology* 72, 533–545.
- SCHTICKZELLE, N., FJERDINGSTAD, E. J., CHAINE, A. & CLOBERT, J. (2009). Cooperative social clusters are not destroyed by dispersal in a ciliate. *Bmc Evolutionary Biology* 9.
- SCHTICKZELLE, N., JOIRIS, A., VAN DYCK, H. & BAGUETTE, M. (2007). Quantitative analysis of changes in movement behaviour within and outside habitat in a specialist butterfly. *Bmc Evolutionary Biology* 7.
- SCHTICKZELLE, N., MENNECHEZ, G. & BAGUETTE, M. (2006). Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology* 87, 1057–1065.
- SCHUPP, E. W., JORDANO, P. & GOMEZ, J. M. (2010). Seed dispersal effectiveness revisited: a conceptual review. Nav Phytologist 188, 333–353.
- SIH, A., BELL, A. & JOHNSON, J. C. (2004a). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* 19, 372-378.
- SIH, A., BELL, A. M., JOHNSON, J. C. & ZIEMBA, R. E. (2004b). Behavioral syndromes: An integrative overview. *Quarterly Review of Biology* 79, 241–277.
- SILVA, M. G. & TABARELLI, M. (2001). Seed dispersal, plant recruitment and spatial distribution of Bactris acanthocarpa Martius (Arecaceae) in a remnant of Atlantic forest in northeast Brazil. Acta Oecologica-International Journal of Ecology 22, 259-268.
- SINERVO, B. & CLOBERT, J. (2003). Morphs, dispersal behavior, genetic similarity and the evolution of cooperation. *Science* **300**, 1949–1959
- SMALLWOOD, K. S., RUGGE, L. & MORRISON, M. L. (2009). Influence of behavior on bird mortality in wind energy developments. *Journal of Wildlife Management* 73, 1082–1098.
- SMITH, D. S., BAILEY, J. K., SHUSTER, S. M. & WHITHAM, T. G. (2010). A geographic mosaic of trophic interactions and selection: trees, aphids and birds. *Journal of Evolutionary Biology* 24, 422–429.
- SMITH, J. B., SCHNEIDER, S. H., OPPENHEIMER, M., YOHE, G. W., HARE, W., MASTRANDREA, M. D., PATWARDHAN, A., BURTON, I., CORFEE-MORLOT, J., MAGADZA, C. H. D., FUESSEL, H. M., PITTOCK, A. B., RAHMAN, A., SUAREZ, A. & VAN YPERSELE, J. P. (2009). Assessing dangerous climate change through an update of the Intergovernmental Panel on Climate Change (IPCC) "reasons for concern". *Proceedings of the National Academy of Sciences of the United States of America* 106, 4133–4137.
- SMOUSE, P. E., FOCARDI, S., MOORCROFT, P. R., KIE, J. G., FORESTER, J. D. & MORALES, J. M. (2010). Stochastic modelling of animal movement. *Philosophical Transactions of the Royal Society B-Biological Sciences* 365, 2201–2211.
- SOLBRECK, C. (1986). Wing and flight-muscle polymorphism in a lygacid bug, Horvathiolus gibbicollis - determinants and life-history consequences. Ecological Entomology 11, 435–444.
- SOLBRECK, C. & SILLENTULLBERG, B. (1990). Population-dynamics of a seed feeding bug, *Lygaeus equestris* .1. Habitat patch structure and spatial dynamics. *Oikos* 58, 199–209.
- SOLOMON, N. G. (2003). A reexamination of factors influencing philopatry in rodents. *Journal of Mammalogy* 84, 1182–1197.
- SOONS, M. B. & BULLOCK, J. M. (2008). Non-random seed abscission, long-distance wind dispersal and plant migration rates. *Journal of Ecology* 96, 581–590.
- SOONS, M. B. & HEIL, G. W. (2002). Reduced colonization capacity in fragmented populations of wind-dispersed grassland forbs. *Journal of Ecology* **90**, 1033–1043.
- SOONS, M. B., MESSELINK, J. H., JONGEJANS, E. & HEIL, G. W. (2005). Habitat fragmentation reduces grassland connectivity for both short-distance and longdistance wind-dispersed forbs. *Journal of Ecology* 93, 1214–1225.
- SOULSBURY, C. D., BAKER, P. J., IOSSA, G. & HARRIS, S. (2008). Fitness costs of dispersal in red foxes (Vulpes vulpes). Behavioral Ecology and Sociobiology 62, 1289–1298.
- SPIEGEL, O. & NATHAN, R. (2010). Incorporating density dependence into the directed-dispersal hypothesis. *Ecology* 91, 1538–1548.
- SRYGLEY, R. B. (2004). The aerodynamic costs of warning signals in palatable mimetic butterflies and their distasteful models. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271, 589–594.
- SRYGLEY, R. B. & ELLINGTON, C. P. (1999). Estimating the relative fitness of local adaptive peaks: the aerodynamic costs of flight in mimetic passion-vine butterflies *Heliconius. Proceedings of the Royal Society of London Series B-Biological Sciences* 266, 2239–2245.
- SRYGLEY, R. B., LORCH, P. D., SIMPSON, S. J. & SWORD, G. A. (2009). Immediate protein dietary effects on movement and the generalised immunocompetence of migrating Mormon crickets *Anabrus simplex* (Orthoptera: Tettigoniidae). *Ecological Entomology* 34, 663–668.

- STAMPS, J. A. (2006). The silver spoon effect and habitat selection by natal dispersers. *Ecology Letters* 9, 1179–1185.
- STAMPS, J. A. & BLOZIS, S. A. (2006). Effects of natal experience on habitat selection when individuals make choices in groups: a multilevel analysis. *Animal Behaviour* 71, 663–672.
- STAMPS, J. A., KRISHNAN, V. V. & WILLITS, N. H. (2009). How different types of natal experience affect habitat preference. *American Naturalist* 174, 623–630.
- STAMPS, J. A. & SWAISGOOD, R. R. (2007). Someplace like home: Experience, habitat selection and conservation biology. *Applied Animal Behaviour Science* **102**, 392–409.
- STENSETH, N. C. & LIDICKER, W. Z. (1992). Animal dispersal: small mammals as a model. Chapman & Hall, London.
- STIRLING, G., FAIRBAIRN, D. J., JENSEN, S. & ROFF, D. A. (2001). Does a negative genetic correlation between wing morph and early fecundity imply a functional constraint in *Gryllus firmus? Evolutionary Ecology Research* 3, 157–177.
- SULLIVAN, J. J. & KELLY, D. (2000). Why is mast seeding in *Chionochloa rubra* (Poaceae) most extreme where seed predation is lowest? *New Zealand Journal of Botany* 38, 221–233.
- TACK, A. J. M. & ROSLIN, T. (2010). Overrun by the neighbors: landscape context affects strength and sign of local adaptation. *Ecology* 91, 2253–2260.
- TANAKA, S. & WOLDA, H. (1987). Seasonal wing length dimorphism in a tropical seed bug - ecological significance of the short-winged form. *Oecologia* 73, 559–565.
- THOMAS, C. D., BODSWORTH, E. J., WILSON, R. J., SIMMONS, A. D., DAVIES, Z. G., MUSCHE, M. & CONRADT, L. (2001). Ecological and evolutionary processes at expanding range margins. *Nature* **411**, 577–581.
- THOMPSON, J. N. (2005). Coevolution: The geographic mosaic of coevolutionary arms races. *Current Biology* 15, R992–R994.
- TRAVESET, A. (1991). Pre-dispersal seed predation in Central-American Acacia famesiana - factors affecting the abundance of cooccurring Bruchid beetles. Oecologia 87, 570–576.
- TRAVESET, A., GULIAS, J., RIERA, N. & MUS, M. (2003). Transition probabilities from pollination to establishment in a rare dioecious shrub species (*Rhamnus ludovici-salvatoris*) in two habitats. *Journal of Ecology* **91**, 427–437.
- TRAVESET, A., RODRIGUEZ-PEREZ, J. & PIAS, B. (2008). Seed trait changes in dispersers' guts and consequences for germination and seedling growth. *Ecology* 89, 95–106.
- TRAVIS, J. M. J., MUSTIN, K., BENTON, T. G. & DYTHAM, C. (2009). Accelerating invasion rates result from the evolution of density-dependent dispersal. *Journal of Theoretical Biology* 259, 151–158.
- VAHL, O. & CLAUSEN, B. (1980). Frequency of swimming and energy-cost of byssus production in *chlamys islandica*. *Journal Du Conseil* **39**, 101–103.
- VAN DER GUCHT, K., COTTENIE, K., MUYLAERT, K., VLOEMANS, N., COUSIN, S., DECLERCK, S., JEPPESEN, E., CONDE-PORCUNA, J. M., SCHWENK, K., ZWART, G., DEGANS, H., VYVERMAN, W. & DE MEESTER, L. (2007). The power of species sorting: Local factors drive bacterial community composition over a wide range of spatial scales. *Proceedings of the National Academy of Sciences of the United States of America* 104, 20404–20409.
- VAN DER JEUGD, H. P. (2001). Large barnacle goose males can overcome the social costs of natal dispersal. *Behavioral Ecology* 12, 275–282.
- VAN DYCK, H. & BAGUETTE, M. (2005). Dispersal behaviour in fragmented landscapes: routine or special movements? *Basic and Applied Ecology*.
- VANDEGEHUCHTE, M. L., DE LA PENA, E. & BONTE, D. (2010). Relative importance of biotic and abiotic soil components to plant growth and insect herbivore population dynamics. *Plos One* 5: e12937.
- VANDER WALL, S. B. & LONGLAND, W. S. (2004). Diplochory: are two seed dispersers better than one? *Trends in Ecology & Evolution* 19, 155–161.
- VANDERWERF, E. A. (2008). Sources of variation in survival, recruitment, and natal dispersal of the Hawai'i 'Elepaio. Condor 110, 241–250.
- VASQUEZ-CASTRO, J. A., DE BAPTISTA, G. C., TREVIZAN, L. R. P. & GADANHA, C. D. (2009). Flight activity of *Sitophilus oryzae* (L) and *Sitophilus zeamais* Motsch (Coleoptera: Curculionidae) and its relationship with susceptibility to insecticides. *Neotropical Entomology* **38**, 405–409.
- VESSBY, K. & WIKTELIUS, S. (2003). The influence of slope aspect and soil type on immigration and emergence of some northern temperate dung beetles. *Pedobiologia* 47, 39–51.
- VIDELER, J. J., WEIHS, D. & DAAN, S. (1983). Intermittent gliding in the hunting flight of the Kestrel, Falco tanuaculus L. Journal of Experimental Biology 102, 1–12.
- VOGWILL, T., FENTON, A. & BROCKHURST, M. A. (2010). How does spatial dispersal network affect the evolution of parasite local adaptation? *Evolution* 64, 1795–1801.
- WENDT, D. E. (1998). Effect of larval swimming duration on growth and reproduction of *Bugula neritina* (Bryozoa) under field conditions. *Biological Bulletin* 195, 126–135.
- WENDT, D. E. (2000). Energetics of larval swimming and metamorphosis in four species of Bugula (Bryozoa). *Biological Bulletin* **198**, 346–356.
- WHITEHOUSE, M. E. A. & JAFFE, K. (1996). Ant wars: Combat strategies, territory and nest defence in the leaf-cutting ant *Atta laevigata*. *Animal Behaviour* 51, 1207–1217.

- WHITTAKER, K. A. & MARZLUFF, J. M. (2009). Species-specific survival and relative habitat use in an urban landscape during the postfledging period. Auk 126, 288–299.
- WIENS, J. D., NOON, B. R. & REYNOLDS, R. T. (2006). Post-fledging survival of northern goshawks: The importance of prey abundance, weather, and dispersal. *Ecological Applications* 16, 406–418.
- WILLIAMS, C. K., LUTZ, R. S., APPLEGATE, R. D. & RUSCH, D. H. (2000). Habitat use and survival of northern bobwhite (*Colinus virginianus*) in cropland and rangeland ecosystems during the hunting season. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 78, 1562–1566.
- WINNE, C. T. & HOPKINS, W. A. (2006). Influence of sex and reproductive condition on terrestrial and aquatic locomotory performance in the semi-aquatic snake *Seminatrix pygaea. Functional Ecology* 20, 1054–1061.
- XIAO, Z. S., HARRIS, M. K. & ZHANG, Z. B. (2007). Acorn defenses to herbivory from insects: Implications for the joint evolution of resistance, tolerance and escape. *Forest Ecology and Management* 238, 302–308.
- YANO, S. & TAKAFUJI, A. (2002). Variation in the life history pattern of *Tetranychus urticae* (Acari : Tetranychidae) after selection for dispersal. *Experimental and Applied Acarology* 27, 1–10.
- YOUNG, A. J., CARLSON, A. A. & CLUTTON-BROCK, T. (2005). Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. *Animal Behaviour* 70, 829–837.
- YOUNG, A. J. & MONFORT, S. L. (2009). Stress and the costs of extra-territorial movement in a social carnivore. *Biology Letters* 5, 439–441.
- YOUNG, O. P. & LOCKLEY, T. C. (1988). Dragonfly predation upon *Phidippus audax* (Araneae, salticidae). *Journal of Arachnology* 16, 121–122.

- ZAGT, R. J. (1997). Pre-dispersal and early post-dispersal demography, and reproductive litter production, in the tropical tree *Dicymbe altsonii* in Guyana. *Journal of Tropical Ecology* 13, 511–526.
- ZERA, A.J. & BOTTSFORD, J. (2001). The endocrine-genetic basis of lifehistory variation: The relationship between the ecdysteroid titer and morphspecific reproduction in the wing-polymorphic cricket *Gryllus firmus. Evolution* 55, 538–549.
- ZERA, A. J. & MOLE, S. (1994). The physiological costs of flight capability in wingdimorphic crickets. *Researches on Population Ecology* 36, 151–156.
- ZERA, A. J., MOLE, S. & ROKKE, K. (1994). Lipid, carbohydrate and nitrogen content of long-winged and short-winged *Gryllus firmus* - Implications for the physiological cost of flight capability. *Journal of Insect Physiology* **40**, 1037–1044.
- ZERA, A. J., SALL, J. & OTTO, K. (1999). Biochemical aspects of flight and flightlessness in Gryllus: flight fuels, enzyme activities and electrophoretic profiles of flight muscles from flight-capable and flightless morphs. *Journal of Insect Physiology* 45, 275–285.
- ZHAO, Z. & ZERA, A. J. (2006). Biochemical basis of specialization for dispersal vs. reproduction in a wing-polymorphic cricket: Morph-specific metabolism of amino acids. *Journal of Insect Physiology* 52, 646–658.
- ZHENG, C. Z., OVASKAINEN, O. & HANSKI, I. (2009). Modelling single nucleotide effects in phosphoglucose isomerase on dispersal in the Glanville fritillary butterfly: coupling of ecological and evolutionary dynamics. *Philosophical Transactions of the Royal Society B-Biological Sciences* 364, 1519–1532.
- ZOLLNER, P. A. & LIMA, S. L. (2005). Behavioral tradeoffs when dispersing across a patchy landscape. *Oikos* 108, 219–230.

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