BIOLOGICAL REVIEWS
Cambridge Philosophical Society

Biol. Rev. (2017), **92**, pp. 1275–1296.
doi: 10.1111/brv.12279

Behavioural synchronization of large-scale animal movements – disperse alone, but migrate together?

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ABSTRACT

Dispersal and migration are superficially similar large-scale movements, but which appear to differ in terms of inter-individual behavioural synchronization. Seasonal migration is a striking example of coordinated behaviour, enabling animal populations to track spatio-temporal variation in ecological conditions. By contrast, for dispersal, while social context may influence an individual's emigration and settlement decisions, transience is believed to be mostly a solitary behaviour. Here, we review differences in drivers that may explain why migration appears to be more synchronized than dispersal. We derive the prediction that the contrast in the importance of behavioural synchronization between dispersal and migration is linked to differences in the selection pressures that drive their respective evolution. Although documented examples of collective dispersal are rare, this behaviour may be more common than currently believed, with important consequences for eco-evolutionary dynamics. Crucially, to date, there is little available theory for predicting when we should expect collective dispersal to evolve, and we also lack empirical data to test predictions across species. By reviewing the state of the art in research on migration and collective movements, we identify how we can harness these advances, both in terms of theory and data collection, to broaden our understanding of synchronized dispersal and its importance in the context of global change.

Key words: dispersal, seasonal migration, social grouping, coalition, budding, transience, sociability, parallel dispersal, schooling, coordinated movement.

CONTENTS

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I. INTRODUCTION

More in depth knowledge on how, why and where individuals move through their environment is fundamental to our understanding of ecological and evolutionary processes, from individual behaviour to metapopulation, meta-community and meta-ecosystem dynamics (Bowler & Benton, 2005; Nathan *et al.*, 2008; Clobert *et al.*, 2009, 2012; Hawkes, 2009; Bauer & Hoye, 2014). This is especially important in the current era of global environmental change because the capacity to move is a vital attribute for tracking shifts in suitable biotic and abiotic conditions (Berg *et al.*, 2010; Baguette *et al.*, 2013).

There is a broad consensus on the main functions of movement: organisms may move (*i*) to satisfy their basic immediate requirements such as food, shelter or mates (‘foraging’ movements), (*ii*) to relocate their home range to a novel area in response to social or environmental stimuli (dispersal), which potentially leads to gene flow, or (*iii*) to escape temporarily adverse environmental conditions through periodic out and back movements (migration). Several attempts have been made to translate this teleological view into more or less exclusive categories in relation to the spatio-temporal scale and the behaviour of the organism, moving within or outside of their usual home range (Ims, 1995; Dingle & Drake, 2007; Dingle, 2014).

Considering the spatio-temporal scale, foraging involves frequent, short-distance (within-patch) movements to locate resources; dispersal occurs at a larger spatial scale and is limited in time to movements from the natal site to the first breeding site (i.e. natal dispersal), or between successive breeding locations (i.e. breeding dispersal); migration is the recurrent, two-way out and back movement of individuals between spatially distinct areas which provide favourable ecological conditions for given periods of time or seasons (Nathan *et al.*, 2008; Hansson & Åkesson, 2014).

Considering behaviour, foraging individuals interrupt their movement within their home range when a suitable food resource is encountered. This also holds true for dispersing individuals, with the difference that dispersing individuals move outside of their current home range to locate a new breeding site. Migrating individuals also move outside of their home range, but their displacements are not necessarily interrupted when they encounter a suitable resource (Dingle & Drake, 2007; Dingle, 2014). Note that these two viewpoints of movement categories are not exclusive (see Section IV for further discussion).

These three main types of movements (foraging, dispersal and migration) are clearly not independent: they all rely on the same locomotory system and, to a lesser extent, on the same orientation, navigation and memory mechanisms (Nathan *et al.*, 2008; Burgess *et al.*, 2016). However, depending on the organism’s life history, one type of movement may be under stronger selective pressures than the others. This may lead to particular morphological and/or physiological specializations of the locomotory and associated systems which may, in turn, constrain the other types of movement (Hansson & Åkesson, 2014).

Although social context is often assumed to be an important external driver of movements, inter-individual dependency during large-scale movement remains poorly understood (Mueller & Fagan, 2008; Nathan *et al.*, 2008; Travis *et al.*, 2012; Bauer & Klaassen, 2013). Dispersal is generally seen as a solitary enterprise. For example, in western mosquitofish (*Gambusia affinis*), individual and population levels of asocial behaviour correlate negatively with schooling behaviour (Cote, Fogarty & Sih, 2012) and positively with dispersal propensity and distance (Cote *et al.*, 2011). As a consequence the influence of the dispersal behaviour of conspecifics on an individual’s dispersal decisions and, in particular, the potential for inter-individual synchronization during dispersal movements, is rarely considered. Indeed, when reviewing the dispersal literature for evidence of collective movements, we found only 42 empirical studies (out of 788 papers between 2000 and 2015) that mentioned key words related to collective dispersal, while six theoretical studies modelled this process (see online Appendix S1). This is in stark contrast with the recent focus on socially informed dispersal (Clobert *et al.*, 2009), where decisions about departure and settlement are based on social cues such as the performance and dispersal behaviour of others (Doligez, Danchin & Clobert, 2002; Doligez *et al.*, 2003; Cote & Clobert, 2007*a*, 2010; Boulinier *et al.*, 2008; De Meester & Bonte, 2010; Fronhofer, Kropf & Altermatt, 2015*b*; Jacob *et al.*, 2015*b*). The widespread occurrence of informed dispersal (Clobert *et al.*, 2009) highlights the need to understand inter-individual synchronization in movements during the dispersal process. Comparison with other large-scale movements, specifically seasonal migration, might be a fruitful way of doing so. Indeed, although dispersal and migration are two superficially similar large-scale movements, they appear to differ in terms of the importance of inter-individual behavioural synchronization. While for many people the word migration commonly conjures up images of enormous caribou herds traipsing a thousand kilometres across the arctic tundra, or massive groups of wildebeest searching for water and seasonal grazing in the East African savannah, animals of almost all species are generally thought to disperse alone. By comparing proximate and ultimate factors driving dispersal and migration, we may understand better when and why we should expect inter-individual behavioural synchronization of one or both types of movement (Fig. 1).

Both dispersal and migration involve three steps: individuals leave their current habitat patch (here defined as an area of sufficient size and resources for an individual to be able to maintain itself for a given period of time: natal or breeding range for dispersal; breeding or wintering range for migration), travel across the landscape (i.e. transience), and finally settle in a novel habitat patch (i.e. settlement: breeding range for dispersal; breeding or wintering range for migration). For both dispersal and migration, inter-individual synchronization, either temporal and/or spatial, may be a specific feature of each of these three movement steps. Certain individuals of a given population may leave their respective habitat patches at the same time (i.e. temporal synchronization). Subsequently, during transience, individuals may travel together (i.e. temporal and spatial synchronization), or use the same path at different times (i.e. spatial synchronization). Finally, individuals may arrive at their destination at the same time (i.e. temporal synchronization) and/or settle in the same habitat patch (i.e. spatial synchronization). Across these three steps, almost all combinations of temporal and spatial synchronization are possible. For example, individuals may leave at the same time, but move towards different locations, or leave at different times, but take the same path across the landscape. Here, we discuss the behavioural components of temporal and spatial synchronization at each step for dispersal and seasonal migration, and we explore how any differences may be linked to the ultimate factors driving dispersal and migration. We subsequently focus on dispersal, highlighting how, until recently, synchronization in movement has largely been ignored in dispersal theory. We emphasize why it is important to consider behavioural synchronization during dispersal, both in terms of our fundamental understanding of ecological and evolutionary processes, as well as for improving predictions of species' responses to current environmental change. Finally, we establish how a synthesis among the fields of dispersal, migration and collective movements may advance our understanding of the social context of inter-individual synchronization in dispersal behaviours, both in terms of developing new theory and collecting empirical data. We thereby identify a new, largely unexplored and potentially crucially important field for future research.

II. DISPERSAL

(1) Synchronization of departure

By dispersing, individuals are able to escape from their abiotic and biotic environment. Specifically, individuals may disperse away from their natal or breeding habitat patch (*i*) to avoid competition with kin and/or non-kin conspecifics and with heterospecifics (Byers, 2000; Lambin, Aars & Piertney, 2001; Le Galliard, Ferriere & Clobert, 2003; Bitume *et al.*, 2013; Fronhofer *et al.*, 2015*a,b*), (*ii*) to avoid mating with related individuals and, hence, inbreeding (Perrin & Mazalov, 2000; Szulkin & Sheldon, 2008) or (*iii*) in response to adverse abiotic and/or biotic conditions (e.g. low resource availability: Byers, 2000; adverse climatic conditions: Bonte *et al.*, 2008; Bestion, Clobert & Cote, 2015; predation risk: Wooster & Sih, 1995; Gilliam & Fraser, 2001; Hakkarainen *et al.*, 2001; McCauley & Rowe, 2010; Bestion *et al.*, 2014). This complex causality generates substantial variation among individuals in dispersal behaviour, for example, in the timing of dispersal. First, different ecological factors may induce individual dispersal at different life stages. For example, high levels of kin competition and/or inbreeding are likely to influence the natal dispersal decision, i.e. prior to reproduction (Cote, Clobert & Fitze, 2007; Szulkin & Sheldon, 2008; Bitume *et al.*, 2013), while variation in population density and/or predation risk may induce dispersal at any life stage, or even affect the dispersal decision in contrasting ways at different life stages (e.g. Le Galliard *et al.*, 2003; Marjamäki *et al.*, 2013). Second, within a given life stage, individuals may experience contrasting local conditions because of spatial and temporal heterogeneity. For example, predators and conspecifics are usually heterogeneously distributed across a given habitat patch (Fryxell *et al.*, 2007). The time needed to assess levels of competition and predation risk will thus vary among individuals. As a consequence, even if individuals ultimately take the same dispersal decision, environmental heterogeneity makes temporal synchronization of departure less likely. Third, dispersal decisions are most often phenotype- and context-dependent, driven by the complex interaction between an individual's phenotype and the prevailing ecological context (Bowler & Benton, 2005; Clobert *et al.*, 2009; Cote *et al.*, 2010; Burgess

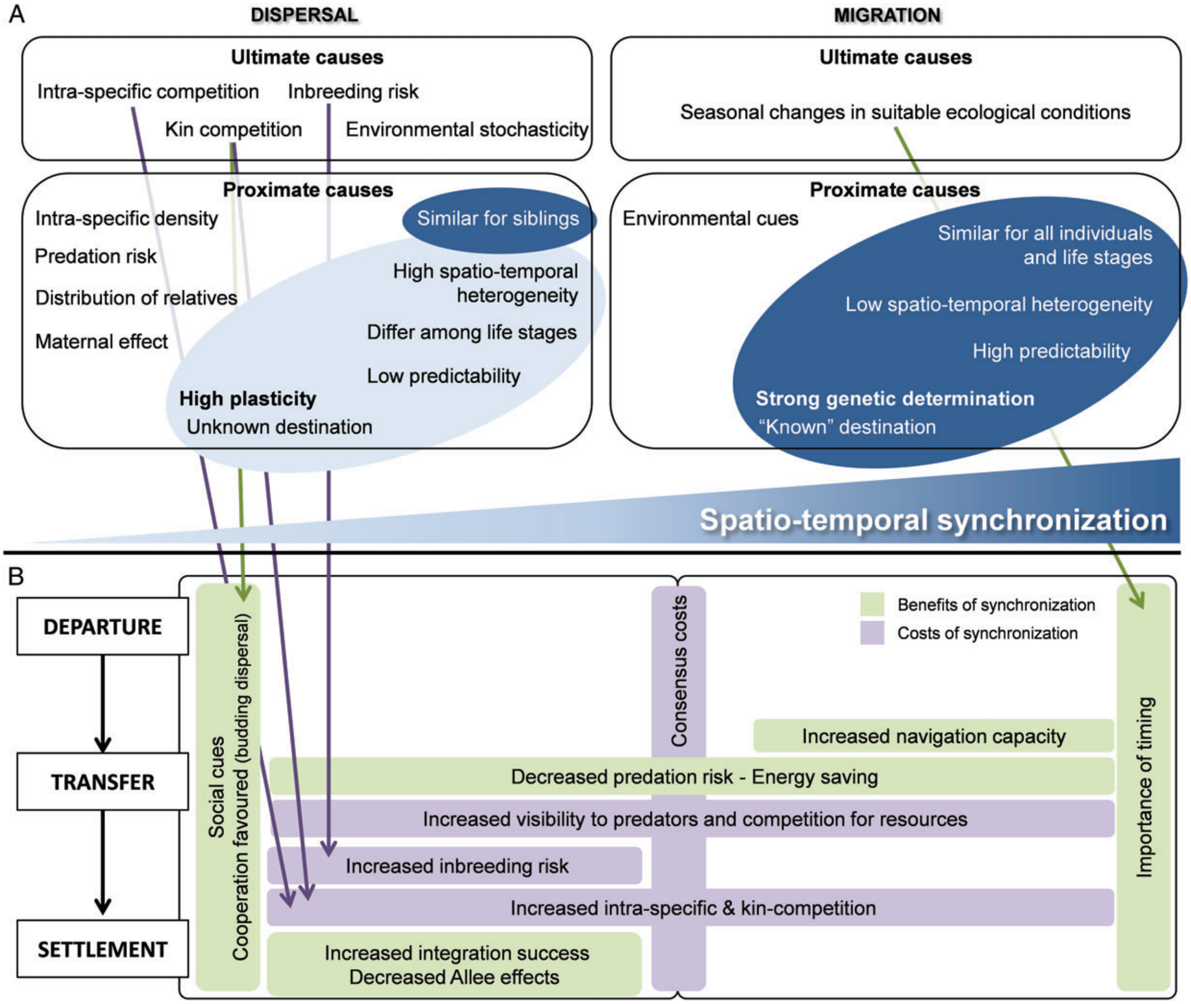

Fig. 1. Overview of the main ultimate and proximate causes of dispersal and migration with the costs and benefits of collective movements. (A) Ultimate and proximate causes of dispersal and migration and their effect on the expected degree of spatio-temporal synchronization of the respective behaviours. For migration, strong genetic determiation and the fact that environmental cues are similar for all individuals, and have low spatio-temporal heterogeneity and high predictability, promote a high degree of synchronization (dark blue). By contrast, for dispersal, the variety of proximate causes and the fact that they differ among life stages and that they exhibit high spatio-temporal heterogeneity and low predictablity, leads to a low degree of synchronization (light blue). However, proximate causes for dispersal are likely to be similar for siblings, thereby promoting somewhat higher synchronization in dispersal decisions among siblings. (B) Costs (purple) and benefits (green) of performing collective behaviours/movements during dispersal and migration across the three stages of departure, transfer and settlement. The arrows from A to B link the ultimate causes of dispersal and migration with the costs and benefits of performing these behaviours collectively. If dispersal evolves as a means of avoiding inbreeding, intra-specific and/or kin competition, we might expect collective dispersal not to be beneficial (purple arrows). However, in cooperative species, budding dispersal (i.e. dispersing with kin) might simultaneously alleviate kin competition and maintain the necessary level of relatedness for cooperation to persist (green arrow). By contrast, migration mainly evolves as a response to seasonal changes in suitable ecological conditions; thus, the timing of the different phases is likely to be crucial for individual fitness and to act on all individuals in similar ways, thereby promoting synchronized behaviours (green arrow).

et al., 2016; Wey *et al.*, 2015; Jacob *et al.*, 2015*a*), including competition, predation risk and abiotic conditions (Byers, 2000; Gilliam & Fraser, 2001; Cote & Clobert, 2007*b*; Bonte *et al.*, 2008; Cote *et al.*, 2013; Pennekamp *et al.*, 2014; Bestion *et al.*, 2015). For example, more active individuals experience higher predation risk (e.g. Yoder, Marschall & Swanson, 2004), while larger individuals are generally better competitors (Garant *et al.*, 2005). The interaction between abiotic and/or biotic conditions and inter-individual phenotypic heterogeneities should thus create asynchrony in the timing of dispersal among individuals, even if they disperse for the same ultimate reason. Overall, the above factors might explain why dispersal is often perceived to be an individual decision rather than a collective one.

However, synchronized dispersal departure has occasionally been observed. The 42 empirical studies from our literature search covered a limited range of taxonomic groups (30 taxa, 1 on nematodes, 15 on arthropods, 2 on fish, 7 on birds, and 12 on mammals), with some dominant taxonomic groups (12 studies on primates). Although these studies mostly involved eusocial species, species with some cooperative behaviours, or species living in groups without overt cooperation ($N = 35$ out of 42 studies), seven studies reported that solitary/non-eusocial species formed groups for at least one dispersal stage. In non-eusocial species, individuals may leave their habitat patch simultaneously and travel in a coordinated manner when local conditions at that given moment in time affect a number of individuals similarly. For example, Burghardt, Greene & Rand (1977) showed that green iguana hatchlings (*Iguana iguana*) often leave their natal patch in groups of 2–10 individuals, moving together in the same direction, because this decreases predation risk. Similarly, in the two-spotted spider mite (*Tetranychus urticae*), a sub-social species, individuals may disperse alone (i.e. walking or ballooning), or collectively (i.e. as a silk ball) under conditions of overcrowding or food shortage (Yano, 2008; Clotuche *et al.*, 2011). Intuitively, individuals that are born within a narrow time window are more likely to experience similar local conditions and so to display temporal synchronization in natal dispersal. This has been well illustrated in marine species (Burgess *et al.*, 2016) where, although dispersal is assumed to be a stochastic process in species with larval forms, it may actually occur in a highly synchronized manner (Leis, 2006; Siegel *et al.*, 2008; Bernardi *et al.*, 2012; Ben-Tzvi *et al.*, 2012; Broquet, Viard & Yearsley, 2013; Burgess *et al.*, 2016; Irisson *et al.*, 2015). Indeed, in these species, the dispersal phases depend on the timing and location of spawning, on vertical migration in the water column, on pelagic larval development and on ocean currents (e.g. Bonhomme & Planes, 2000; Strathmann *et al.*, 2002; Pringle *et al.*, 2014; Burgess *et al.*, 2016). A single individual, and even multiple individuals, often release all their gametes or larvae into the water at the same time (Shapiro, 1983; Alino & Coll, 1989; Mercier & Hamel, 2010). For broadcast spawners, releasing sperm and eggs, synchronized releases may increase the aggregation of gametes and therefore the success of fertilization (Levitan, Sewell & Chia, 1992) or may be triggered by environmental factors (Alino & Coll, 1989; Mercier & Hamel, 2010). The release of eggs or larvae may also be synchronized in brooders because of external conditions that may synchronize spawning or may enhance progeny survival prospects, e.g. using the ebbing tide to flush eggs and larvae away from benthic predators or nearshore environments not conducive to pelagic larval development (Alino & Coll, 1989; Nakai *et al.*, 1990; Mercier & Hamel, 2010). These synchronized releases could result in passively synchronized dispersal departure. In addition, candidate dispersers may actively postpone their departure until environmental conditions are optimal in order to increase their dispersal success which should also favour temporal synchronization in departure.

Actively synchronized departure appears to be more common among both invertebrates and vertebrates of eusocial and cooperative species. An extreme example is group fission, where an increase in group size or severe external conditions leads to the splitting of a single group or entity into two or more groups, often, but not always, based on relatedness (Lefebvre, Ménard & Pierre, 2003; Rangel, Griffin & Seeley, 2010). For example, in social insects, colonies reproduce by fission where a part of the population (e.g. old queen and workers) flies together in a swarm to locate a new nest site, with take-off being induced by signals from nest-site scouts (Rangel *et al.*, 2010).

A somewhat less striking example concerns coalitions in cooperative species. In many cooperative breeders, offspring delay dispersal and become helpers (Cockburn, 1998; Hatchwell, 2009). Subsequently, some individuals may disperse alone or in small coalitions to become helpers or breeders in neighbouring groups (Bergmüller *et al.*, 2005; Wikberg *et al.*, 2014). Dispersal coalitions are also often made up of related individuals (Sharp, Simeoni & Hatchwell, 2008; Wikberg *et al.*, 2014). For example, Sharp *et al.* (2008) observed kin coalitions and kin-biased helping in dispersing long-tailed tits (*Aegithalos caudatus*). Similarly, in cooperatively breeding brown jays (*Cyanocorax morio*), related males formed coalitions and dispersed to groups with other male relatives (Williams & Rabenold, 2005). These kin coalitions increase the probability of gaining access to reproduction and reduce the costs of integrating into another group (Heinsohn *et al.*, 2000; Williams & Rabenold, 2005; Sharp *et al.*, 2008; Ridley, 2012; van Dongen *et al.*, 2014, reviewed in Hatchwell, 2009).

At a proximate level, siblings generally share a common pre-dispersal environment, including the maternal environment and the levels of inbreeding and kin competition, and often display phenotypic similarities (i.e. family effects, *sensu* Gaillard *et al.*, 1998). In addition, siblings are born in the same location and share the same potential dispersal destinations. We would thus expect siblings to take similar dispersal decisions with similar timing; however, there is virtually no empirical information on the dispersal behaviour of siblings in wild populations. Some preliminary data from a detailed long-term study of roe deer (*Capreolus capreolus*) (see Debeffe *et al.*, 2012, for details) on the dispersal fates of twin litter-mates monitored by GPS telemetry indicated some degree of synchronization in dispersal behaviour within litters, but this synchronization was never both spatial and temporal together. While litter mates generally made the same dispersal decision, either to disperse or to remain philopatric, and left the natal range at approximately the same time (i.e. during the same week), in most cases synchronization during transience and settlement was low or absent. Hence, natal dispersal of roe deer seems to be essentially an asocial behaviour, even among litter mates, which contrasts with the highly synchronized migration behaviour observed in certain populations of the same species (Danilkin & Hewison, 1996). This lack of synchronization in the settlement behaviour of dispersing siblings is coherent with the hypothesis that natal and breeding dispersal are largely driven by selection for inbreeding avoidance in this generally highly sedentary species (Debeffe *et al.*, 2014).

The dispersal of kin coalitions, also called budding dispersal, has some theoretical support and has been hypothesized to promote the evolution of cooperation.

Limited dispersal is believed to favour the evolution of cooperation (Hamilton, 1964; Schtickzelle *et al.*, 2009) but, at the same time, to increase competition among relatives (West, Pen & Griffin, 2002). This means that dispersal should have little or no influence on the evolution of cooperation. Budding dispersal, where related individuals disperse in groups, may favour cooperation because it decreases kin competition while maintaining high levels of relatedness (Krushelnycky, Loope & Joe, 2004; Gardner & West, 2006; Kümmerli *et al.*, 2009; Hui & Pinter-Wollman, 2014; Koykka & Wild, 2015).

(2) Temporal synchronization in transience and settlement

The temporal synchronization of departure, transience and settlement should be strongly interconnected. Temporal synchronization of transience and settlement probably only occurs when departure is also synchronized in time, whereas synchronized departure does not always lead to synchronized transience. Budding dispersal in cooperative species almost always involves leaving, travelling and settling together (Cockburn, 1998; Hatchwell, 2009), while dispersal in response to common local conditions is more likely to lead to synchronized departure only. However, synchronized transience may also result from similarities in environmental drivers of dispersal. For example, synchronized spawning in aquatic species may lead to similarities in the direction or the distance moved when the dispersal path is driven by environmental factors as in passive dispersers (e.g. ocean currents: Pringle *et al.*, 2014) or when active dispersers coordinate their behaviour during transience (Leis, 2006; Irisson *et al.*, 2015). There is some indirect evidence that larvae may disperse together (Bernardi *et al.*, 2012; Ben-Tzvi *et al.*, 2012; Shima & Swearer, 2016). For instance, using otolith micro-chemistry, Ben-Tzvi *et al.* (2012) showed that larvae of the coral-reef damselfish *Neopomacentrus miryae* likely remain in cohesive cohorts of unrelated individuals during the 28 days of dispersal, from hatching to settlement.

Travelling and settling in groups is associated with benefits (e.g. decreased predation risk, higher integration success) and costs (e.g. consensus costs) which are similar in nature to those of group living (Krause & Ruxton, 2002; Conradt & Roper, 2005; Couzin *et al.*, 2005). Animals travelling in groups may benefit both directly and indirectly from the presence of other group members. More experienced individuals may, for example, improve group navigation (Simons, 2004). Some individuals from a group may also have valuable information, such as knowledge of the location of a food source or a safe movement route (Couzin *et al.*, 2005). Benefiting from the knowledge and experience of conspecifics is frequent in social insect movement (Rangel *et al.*, 2010). Animals travelling in a group can also benefit from the presence of conspecifics by saving energy during movements, such as formation flying in birds (Weimerskirch *et al.*, 2001), or schooling in fish (Herskin & Steffensen, 1998), or by increasing time spent foraging through decreasing vigilance when foraging in a group (Krause & Ruxton, 2002). Group formation can also spread predation risk across multiple individuals, enhance predator avoidance, or improve defensive strategies such as the mobbing of predators (reviewed in Krause & Ruxton, 2002). On the other hand, moving in groups involves costs such as increased competition for resources (Valone, 1989), slower movement if groups have to adjust their speed to the slowest individuals, and consensus costs (Conradt & Roper, 2005). Groups can also be much more vulnerable to extrinsic threats like mortality from accidental events (Bleich & Pierce, 2001), and can also be easily detected and therefore vulnerable to exploitation (Sala, Ballesteros & Starr, 2001).

Synchronized settlement is well documented in schooling larval fishes (Breitburg, 1989; Leis, 2006). Even in species with no schooling behaviour at an adult stage, larvae of several benthic fish species start schooling in a more or less advanced larval stage before they settle (Leis, 2006). This schooling behaviour during the transience and settlement phases allows larvae to swim faster and in a straighter direction, as shown in the common pomacentrid damselfish *Chromis atripectoralis* (Irisson *et al.*, 2015), and therefore may reduce the high dispersal costs levied in such environments. Grouped individuals might also achieve higher settlement success compared to lone individuals. When lone immigrants settle in an unfamiliar habitat, they might have difficulty finding resources (food, shelter), identifying potential risks (e.g. predators), or being accepted by locally resident individuals (i.e. integration costs: Bonte *et al.*, 2012). The benefits of dispersal coalitions during settlement have been well studied in several cooperative species. Coalitions provide allies for competition with unfamiliar individuals, increasing the likelihood of successful reproduction (Heinsohn *et al.*, 2000; Ridley, 2012). Interestingly, some social species display both solitary and coalition dispersal (Heinsohn *et al.*, 2000; Yano, 2008; Ridley, 2012), providing a promising model for evaluating the costs and benefits of the two dispersal modes.

For example, the cooperativly breeding Arabian babbler *Turdoides squamiceps* can disperse both individually or in coalitions (Ridley, 2012). Interestingly, individuals typically disperse alone when moving into a group with a breeding vacancy, but may disperse as same-sex coalitions when moving into a group where there is no breeding vacancy. Dispersing as a coalition has costs, the main one being that after settlement the coalition breaks down and typically only one individual becomes the dominant breeder, so that the others must disperse again. Coalition dispersal is, therefore, clearly not advantageous when breeding vacancies are available. However, the benefits outweigh the costs when dispersers must integrate into a saturated breeding group, evicting the residents. In this case, larger coalitions have a higher chance of evicting residents, while participating indivduals lose less body mass as a result of dispersal costs. Individuals in the coalition, therefore, increase their own chance of becoming breeders. Interestingly, despite there being no evidence for dispersal polymorphisms, Ridley (2012) showed a high degree of individual repeatability in solitary *versus* coalition dispersal tactics.

Similarly, the two-spotted spider mite *Tetranychus urticae* can disperse alone, either actively walking or being passively transported by other organisms or by wind (ballooning), or collectively, by forming silk balls that are transported by wind. Clotuche *et al.* (2011, 2013) recently elucidated some of the mechanisms and cost/benefit ratios involved in collective dispersal *via* silk balls. Typically, solitary dispersal is performed by mated females, while silk balls are mostly composed of immature individuals of both sexes. Moreover, the formation of silk balls seems to be triggered by food shortage and high population density. Passive dispersal, especially air-borne, has clear costs as the destination is completely out of the organism's control. Individuals have, therefore, a high chance of settling in unsuitable habitat. Additionally, when dispersing alone in areas where mates are not available or scarce, individuals settling in suitable habitat are prone to Allee effects. Clotuche *et al.* (2013) not only showed that silk balls mainly contain immature stages, but also that individuals do not segregate according to relatedness or sex. Moreover, silk balls help to reduce the risk of dessication during ballooning. However, silk balls also involve a high cost as individuals in the inner part of the ball usually die. Collective dispersal through silk balls seems, therefore, to be a good means for colonizing new areas for this species, as the risk of Allee effects and inbreeding are reduced in newly founded populations.

These two examples clearly exemplify how the balance between costs and benefits of solitary *versus* collective dispersal depends on an individual's stage, phenotype and on social as well as ecological conditions. We might, therefore, expect the frequency of alternative tactics within a population to shift in response to changes in the environment that make collective dispersal more or less advantageous. For example, for the Arabian babbler, we might expect more frequent coalition dispersal during severe climatic conditions (high cost of solitary dispersal), or in highly saturated habitats (Ridley, 2012). In the same way, if the propensity for collective dispersal has a strong genetic component, we might expect directional changes in ecological conditions to exert selective pressure to either increase or decrease the frequency of collective dispersal. For instance, in fragmented landscapes, dispersal costs are higher because dispersers are more visible to predators and the probability of finding a suitable habitat patch is lower (Bonte *et al.*, 2012). Hence, the occurrence and evolution of dispersal coalitions in these types of landscape should vary in relation to the costs and benefits of anti-predator defence (i.e. dilution and diversion effects *versus* visibility to predators) and information gathering (i.e. amount of information *versus* inaccurate information). Studies on recently fragmented or currently expanding populations, coupled with the development of eco-evolutionary theory on collective dispersal in fluctuating environments would be extremely useful to shed new light on when and where we should expect collective dispersal to evolve.

(3) Spatial synchronization in transience and settlement

Although temporal synchronization in dispersal appears to be virtually exclusive to social and marine species, spatial synchronization among dispersers might be more common. In some species, solitary dispersers follow the same dispersal path and settle in the same place as other members of the same initial population. Dispersal behaviour has been shown to have both genetic and maternal determinants (Pasinelli, Schiegg & Walters, 2004; Braendle *et al.*, 2006; Sinervo *et al.*, 2006; Tschirren, Fitze & Richner, 2007). In addition, siblings share the same birth location and the same potential destinations (Matthysen, Van de Casteele & Adriaensen, 2005) and are subject to the same maternal effects, including parental care (Matthysen *et al.*, 2010). Therefore siblings may disperse similar distances (Pasinelli *et al.*, 2004) and/or in the same direction (Matthysen *et al.*, 2005), so that related individuals settle closer to each other than unrelated individuals (Matthysen *et al.*, 2005, 2010; Williams & Rabenold, 2005; Bernardi *et al.*, 2012). Independently of similarities in dispersal distance and direction, kin may form aggregated settlements following dispersal as shown in ascidians (Grosberg & Quinn, 1986; Aguirre *et al.*, 2013). For instance, in the sessile colonial ascidian *Botryllus schlosseri*, larvae settle in kin aggregations and this settlement pattern cannot be explained only by dispersal distance (Grosberg & Quinn, 1986).

Non-kin individuals might also display a degree of spatial synchronization in their dispersal behaviour because individuals may use abiotic and biotic cues to locate suitable high-quality habitats including the location of conspecifics (Stamps, 2001). By doing so, individuals may benefit indirectly from the presence of conspecifics. Animals may be able to assess environmental quality through the presence of conspecifics without paying the costs of detailed exploration. For example, Luschan's salamanders (*Lyciasalamandra antalyana*) use chemical scents deposited by conspecifics to identify a safe shelter (Gautier *et al.*, 2006). Using other individuals to assess environmental conditions is particularly useful in situations when animals have limited exploration capacity during migration or dispersal (Cote, Boudsocq & Clobert, 2008). For example, individuals in several arthropod species follow tracks left by previous dispersers, using them as cues to identify potentially suitable dispersal trajectories (Yano, 2008; Fernandez, Hance & Deneubourg, 2012). Similarly, intertidal gastropods are known to follow mucus trails left by conspecifics (Erlandsson & Kostylev, 1995; Hutchinson *et al.*, 2007) and this trail-following behaviour may explain similarities in the direction of dispersal among individuals (Chapman, 1986). Dispersers may also use conspecific cues to select their new home range. In the gregarious tubeworm (*Hydroides dianthus*), larvae display a dispersal polymorphism, with a small proportion of larvae settling in uninhabited substrata while the majority settle in existing aggregations (Toonen & Pawlik, 2001). This dispersal polymorphism has a significant genetic basis and is suggested to be maintained through a fitness benefit–cost balance. This mixed strategy, with a few asocial risk takers acting as colonizers and many social risk avoiders that join established colonies, may improve the speed of range expansion and invasion (Cote *et al.*, 2010; Fogarty, Cote & Sih, 2011). This type of spatially synchronized, but temporally distinct, collective movement seems to be widespread and not restricted to eusocial species. However, there is, to date, little empirical information available because studying such processes requires detailed monitoring of dispersal paths at the individual level, which is often difficult.

(4) Spatial and temporal synchronization across dispersal steps

The dispersal of semelparous organisms across regions, and even continents, particularly butterflies and moths, provides a clear example of extensive behavioural synchronization across the three steps of dispersal. Gene flow at this scale is dependent on a strong level of synchronization in departure, transience and settlement which underlies the multi-generational process required to achieve this fascinating coordinated dispersal of millions of individuals (e.g. Chapman, Reynolds & Wilson, 2015). However, as these specific examples have traditionally been considered within the evolutionary framework of migration, we will discuss them in Section IV.

Similarly, in marine species, synchronization of the entire dispersal process may occur, for example, when spawning is temporally and spatially limited or when it varies in relation to environmental gradients (e.g. Morgan, 1990; Hovel & Morgan, 1998). Collective dispersal, when kin or non-kin larvae that spawned at the same time are transported together and settle at the same site, is therefore likely, as suggested by the few available empirical and theoretical studies of this system (Selkoe *et al.*, 2006; Siegel *et al.*, 2008; Broquet *et al.*, 2013). A few empirical studies further suggested that collective dispersal, from hatching to settlement, may result from active schooling behaviour in marine larval fish (Bernardi *et al.*, 2012; Ben-Tzvi *et al.*, 2012; Shima & Swearer, 2016).

To conclude, because of the multiple determinants involved, dispersal is often perceived to be a solitary movement. However, it appears that temporal and/or spatial synchronization is less unusual than previously thought, at least for semelparous, social and marine species, and can even be observed unexpectedly in certain organisms. For example, in the nematode *Pristionchus pacificus*, larvae search for a new host by standing on their tail and waving their body to attach to a larger animal vector (Penkov *et al.*, 2014). Surprisingly, larvae produce an adhesive lipid that facilitates the congregation of multiple individuals into a tall nematode tower-like structure. This waving tower probably maximizes the probability of attaching to a vector and results in collective host finding (Penkov *et al.*, 2014). With the exception of these intriguing examples, dispersal synchronization might be more common particularly for siblings, because they share both their environmental context (maternal and post-natal) and their genes.

While eusocial species make up the majority of examples, synchronized dispersal also occurs in several other 'non-social' taxa. For example, in several aquatic species, larvae may undergo synchronized departure, transience and/or settlement. As in passively dispersing species, abiotic factors (e.g. wind and ocean currents) may result in the movement of a large part of the population in a synchronized manner. However, larvae may also actively school during transience or settlement, even though adults of the same species do not necessarily school (Leis, 2006). Collective dispersal may have evolved because of benefits similar to those obtained from grouping in other contexts such as feeding (e.g. reduced predation, better navigation and orientation) in social and non-social species while the costs of sociality may be higher than the benefits outside of the dispersal stage for non-social species. Aside from grouping benefits, synchronized movements may also result from sharing an abiotic or biotic vector in passively dispersing species (Fragoso, 1997; Nathan & Muller-Landau, 2000; Mazé-Guilmo *et al.*, 2016).

III. SEASONAL MIGRATION

(1) Synchronization of departure

Seasonal migration is a widespread behaviour that enables animal populations living in highly seasonally variable environments to track spatio-temporal variations in suitable ecological conditions through the two-way movement of individuals back and forth between areas providing seasonally favourable environments (Lucas *et al.*, 2001; Alerstam, Hedenstrom & Akesson, 2003; Milner-Gulland, Fryxell & Sinclair, 2011; Avgar, Street & Fryxell, 2014). Seasonal migration provides some of the most striking examples of coordinated behaviour in the animal kingdom, involving large numbers of individuals that move together through time and space in a synchronized fashion (Lucas *et al.*, 2001; Hubbard *et al.*, 2004; Hinch *et al.*, 2005; Milner-Gulland *et al.*, 2011). Although this kind of mass migration is common, migration is in fact a diverse assemblage of movement types, including strongly spatially and temporally synchronized movements, solitary movements and partial migration, where only some individuals in a given population migrate (see references below).

The benefits of migration clearly revolve around the exploitation of spatial and temporal variation in food availability, climatic conditions, predation risk, or a combination of several of these factors (Chesser & Levey, 1998; Boyle & Conway, 2007; Shaw & Couzin, 2013; Avgar *et al.*, 2014). For instance, in marine and freshwater species, migration is defined as movements that result in an alternation between habitats used for reproduction, feeding or refuge with a regular periodicity within an individual's lifetime (Northcote, 1978; Lucas *et al.*, 2001; Binder, Cooke & Hinch, 2011). All individuals of a given population should experience similar seasonal variation in conditions and should, therefore, initiate their migratory movement during a short time window. This underlies why migration is often defined as a synchronized movement of a large part of a population (Lucas *et al.*, 2001; Binder *et al.*, 2011). This temporal synchronization should be particularly strong when suitable environmental conditions for migration are temporally restricted (Duriez *et al.*, 2009). For example, arctic-nesting capital breeders have a narrow window for breeding which might explain why spring migration is more synchronized than autumn migration back to the wintering ranges (Madsen, Cracknell & Fox, 1999). Furthermore, individuals generally do not wait until environmental conditions deteriorate to leave because to do so may decrease the energy available for migration, and/or because late arrival at the wintering range may decrease their competitive ability (Alerstam *et al.*, 2003; Milner-Gulland *et al.*, 2011). For example, some species migrate in order to track gradual changes in environmental gradients, e.g. plant phenology for herbivorous birds and ungulates (i.e. surfing the green wave: Bischof *et al.*, 2012; van Wijk *et al.*, 2012), rather than hopping between spatially distinct seasonal ranges. This anticipation of changes in environmental conditions further intensifies the temporal synchronization of departures within a given population. The initiation of migration should therefore be linked to early warning signs, or proxies, of habitat deterioration, or to an internal clock mechanism (Hinch *et al.*, 2005; Pulido, 2007; Ramenofsky & Wingfield, 2007). As a consequence, migration is facilitated by a variety of behavioural and physiological adaptations, also known as a migration syndrome, which may be under genetic and/or environmental control (Ramenofsky & Wingfield, 2007; Hedenström, 2008; Binder *et al.*, 2011; Liedvogel, Åkesson & Bensch, 2011). For example, diadromous fish migrating between seawater and freshwater environments display physiological adaptations to overcome this osmoregulatory challenge (Hinch *et al.*, 2005). Another interesting adaptation is the ability to modify social behaviour so that species which are usually territorial are able to form large social groups for migration (Danilkin & Hewison, 1996; Alerstam *et al.*, 2003). For example, roe deer males are strictly seasonally territorial, with very low levels of gregarity, and disperse as single individuals (Debeffe *et al.*, 2012), but in marginal parts of their range (e.g. Siberia), they migrate in large groups in a more or less synchronized mass long-distance movement (Danilkin & Hewison, 1996). Similarly, humpback whales (*Megaptera novaeangliae*), which are largely solitary, can be transiently involved in cooperative behaviours including migrating in small kin-biased groups (Valsecchi *et al.*, 2002).

The seasonal shifts in environmental conditions which initiate migration are, however, not entirely predictable and may be largely gradual. As a result, there must be some flexibility in the migration syndrome (Ramenofsky & Wingfield, 2007; Binder *et al.*, 2011), which may explain intra-population variation in the timing of migration (Lucas *et al.*, 2001; Craig *et al.*, 2003). For example, because the initiation of migration depends on social interactions, environmental cues and hormonal regulation, the timing of migration may vary among individuals or classes of individuals (i.e. differential migration). Many migratory species show some intra-population variation in migration timing which may reflect phenotypic variation driven by either genetic variation or differences in environmental conditions (Noordwijk *et al.*, 2006). For example, in southern German blackcap (*Sylvia atricapilla*), migration traits (e.g. tendency, timing, distance) are heritable and a selection experiment demonstrated that migratory strategies can be completely modified following two generations of selection (Pulido *et al.*, 2001; Pulido, 2007; Pulido & Berthold, 2010). Migration timing may also vary over the lifetime or among life stages. For example, migration timing in humpback whales varies with age, sex and reproductive status (Craig *et al.*, 2003). Within-population differences in migratory traits can result in different migration patterns (Lucas *et al.*, 2001). For example, in the roach (*Rutilus rutilus*), individual migrants vary consistently in the timing of their migration over multiple seasonal migratory events (Brodersen *et al.*, 2012), while in bar-tailed godwits (*Limosa limosa baueri*) in New Zealand, individuals leave within the same week each year, resulting in high among-year repeatability of migration behaviour (Battley, 2006).

An extreme and widespread form of intra-population variation in migratory behaviour is partial migration, where only a fraction of a given population migrates (Lundberg, 1988; Chapman *et al.*, 2011*a*). Partial migration has been well documented in birds, mammals, arthropods, amphibians and fish, providing clear examples of what could be considered as an extreme form of unsynchronized migration behaviour (Lundberg, 1988; Hendry *et al.*, 2004; Chapman *et al.*, 2011*a*). The propensity to migrate may vary among genotypes (Snyder, 1991; Lucas *et al.*, 2001; Páez *et al.*, 2011), age, size or sex classes (Grayson & Wilbur, 2009; Páez *et al.*, 2011), or with local environmental conditions such as temperature, density, food availability or predation risk (Olsson *et al.*, 2006; Grayson & Wilbur, 2009; Griswold, Taylor & Norris, 2011). Variation among individuals in competitive ability and/or vulnerability to predation may lead to the expression of distinct migratory strategies. For example, Brönmark *et al.* (2008) developed a model to explore how a growth rate–predation risk trade-off could affect partial migration in roach (*Rutilus rutilus*). The winter migration of cyprinids from lakes to streams is explained by a higher ratio of predation risk to food availability (i.e. a cost/benefit ratio) in lakes than in streams during winter (Brönmark *et al.*, 2008). However, all individuals within a population are not equal with respect to vulnerability to predators and foraging rate and this may explain observed inter-individual differences in migratory behaviour (Chapman *et al.*, 2011*b*). In elk (*Cervus elaphus*) of the Ya Ha Tinda herd near Banff National Park, alternative migratory strategies are maintained: in comparison to resident elk, migrant elk increase their reproductive success through access to higher forage quality, but at the cost of lower survival due to wolf predation (Hebblewhite & Merrill, 2011). As a result, there is almost no difference in demographic performance between migratory and resident groups; hence the two tactics are maintained in the population.

(2) Synchronization in transience and arrival

Dispersal typically involves an unknown destination, hence, synchronization in transience and settlement during dispersal are possible almost exclusively when departure is also synchronized. However, in long-lived iteroparous species, migration is often orientated towards the same location year after year, so that although migrants do not always leave together, they may converge en route or arrive at the same destination. Indeed, although migration commonly conjures up an image of large groups of individuals leaving their summer ranges together, travelling across the landscape as a single unit and arriving in their wintering areas together, synchronization of migratory initiation and transience may be completely unconnected. For example, individuals that leave a given range separately may follow similar, or different, alternative migration paths, but arrive in the same wintering area (Åkesson & Hedenström, 2007; Horton *et al.*, 2011). The migration of Siberian roe deer typifies this case, where groups of various sizes leave their summer ranges in successive waves over a period of about one month in early autumn. They then follow broadly similar migration routes which are also consistently used from one year to the next, travelling over 100 km during 3–4 weeks, crossing major rivers at particular points, and finally settling in neighbouring winter ranges (Danilkin & Hewison, 1996).

The migratory path an individual takes will depend first on its orientation and navigational skills. Successful migration requires the ability to detect and interpret olfactory cues, the Earth's magnetic field, a sun compass and/or landmarks, abilities that are likely genetically and/or culturally inherited (Lucas *et al.*, 2001; Alerstam *et al.*, 2003; Åkesson & Hedenström, 2007; Binder *et al.*, 2011; Horton *et al.*, 2011). However, when migration is based on a more incremental tracking of suitable conditions, the ability to interpret environmental cues may be more important (van Wijk *et al.*, 2012). The speed at which an animal travels during migration also depends on its maximal locomotion speed, its rate of energy consumption/refuelling and its ability to use external cues (Hedenström, 2008). Each of these traits may be under genetic and/or environmental control (Åkesson & Hedenström, 2007; Ramenofsky & Wingfield, 2007; Binder *et al.*, 2011), so that the direction, speed and distance of a migration event may vary within and among species and populations (Noordwijk *et al.*, 2006). First, individuals vary in their ability to deal with external factors (e.g. landscape barriers, wind), with the result that they may move in different directions (Gschweng *et al.*, 2008). For example, in Northern wheatears (*Oenanthe oenanthe*), birds in good condition migrate directly towards their breeding areas, crossing the sea, whereas birds in poor condition migrate towards nearby mainland areas because of lower fuel availability (Schmaljohann & Naef-Daenzer, 2011). Similarly, migrating individuals may choose their stop-over sites in relation to the prevailing conditions in their habitat of origin (Végvári *et al.*, 2011). Second, independently of locomotion speed itself, migration speed also depends strongly on fuelling rate and energy consumption during locomotion, both of which may vary with individual phenotype. Among-species comparison shows that migration speed and distance is maximal in small-sized birds compared to large-sized birds, and this might also hold true among individuals within species (Alerstam *et al.*, 2003; Åkesson & Hedenström, 2007). These patterns may explain the degree of consistency in the duration of migration such as that observed in greater snow goose (*Anser caerulescens atlanticus*; Bety, Giroux & Gauthier, 2004). Finally, migration distance may also vary among individuals of a given population, so that they choose different wintering or summering locations. This can result from variation in the direction and/or speed of migration. Six years of monitoring of roach migration showed that individuals had a consistently high level of site fidelity to their wintering ranges (Brodersen *et al.*, 2012). Indeed, migratory traits (timing, speed, distance, direction) often vary among individuals in a more or less consistent way (Bety *et al.*, 2004; Phillips *et al.*, 2005; Vardanis *et al.*, 2011; Brodersen *et al.*, 2012), so that asynchrony in migration behaviour may persist at the population level. However, within the context of social information-based strategies (e.g. scroungers–producers), some individuals may rely more on the movement and navigational skills of others rather than on their own capabilities (Guttal & Couzin, 2010), thereby reinforcing temporal synchronization among migrants. For example, Guttal & Couzin's (2010) model predicted that individuals that use environmental cues during migration should be exploited by social information users.

To conclude, seasonal migration has less labile drivers than dispersal, notably large-scale and fairly predictable environmental shifts (e.g. seasonal cycles). The timing of migration departure and arrival can have strong fitness consequences (e.g. on reproductive success). As a result, migration behaviours most often show a high degree of genetic determinism (Pulido, 2007), although there are non-trivial levels of inter-individual variation. Together, these factors might explain why migratory movements are generally synchronized within groups of individuals, or even among different groups.

IV. SEASONAL MIGRATION AND DISPERSAL: INTER-CONNECTED MOVEMENTS?

Dispersal and seasonal migration are two large-scale movements which both involve an individual moving outside of its normal home range and/or natal site. This may be why dispersal is sometimes referred to as a migratory strategy (Dingle & Drake, 2007; Chapman *et al.*, 2015) and why these behaviours are often discussed together, creating some historical controversy (Kokko & Lundberg, 2001; Winkler, Greenberg & Marra, 2005; Nathan *et al.*, 2008).

(1) A teleological view of movement

Classifications of movements based on either spatio-temporal scale or behaviour (see Section I) are clearly not exclusive; nonetheless they represent different points of view that have created decade-long controversy in the field of the evolutionary ecology of large-scale movements. One main source of misunderstanding stems from the fact that individuals and species can have very different strategies of space use due to differences in their life histories. A useful distinction was proposed by Mueller & Fagan (2008) who described three broadly contrasted lifestyles: sedentary, migratory and nomadic. (*i*) Sedentary individuals spend most of their lifetime in the same area (i.e. home range). In sedentary organisms, movements leading to gene flow (i.e. dispersal) are rare events in the lifetime of an individual and are dependent mainly on the social context. (*ii*) Migratory individuals generally occupy environments with predictable seasonal fluctuations and perform regular, recurring long-distance movements between spatially disjoint ranges. (*iii*) Nomadic individuals are not strongly faithful to any particular range or area. Rather, they exhibit extremely long lifetime tracks (i.e. the cumulative distance travelled by an individual during its life; Baker, 1978), continuously moving across the landscape in a non-regular fashion, mainly in response to highly unpredictable environmental conditions and/or resource distribution (Andersson, 1980; Allen & Saunders, 2002; Mueller & Fagan, 2008; Börger *et al.*, 2011; Jonzén *et al.*, 2011; Mueller *et al.*, 2011). Thus, the way in which foraging, dispersal and migration movements are expressed during the organism's life cycle is clearly dependent on these three different lifestyles so that the definitions of these different movement types varies depending on the organism concerned. In particular, confusion arises when long-distance movements occur across generations, or for organisms which adopt the less well understood nomadic lifestyle.

For example, in semelparous organisms (individuals that reproduce only once in their lifetime), some species display periodic changes in their distribution at the regional or continental scale as an evolutionary response to environmental degradation. The similarity of this process, typical of many invertebrates, and particularly well documented in insects (e.g. Chapman *et al.*, 2015), to seasonal migration has led to an alternative view of migration. In such organisms, the round trip is the result of a family affair: individuals that come back to the starting point of the 'migration' process are the descendants of those that engaged in 'migration' usually one or several generations before. Selection on migration should thus occur at the level of the group or deme. We suggest that a more evolutionarily relevant explanation of the multi-generational movements of semelparous individuals should focus on the relative costs and benefits at the individual level. In the northern hemisphere worldwide, butterflies and moths that overwintered in the southern part of the species' distribution range fly northwards in spring, colonizing areas where hibernation is not possible due to the cold climate. They mate and reproduce there, sometimes several hundred kilometres from their departure point, and after development their offspring engage in the same kind of northwards long-range movements. At mid-summer, when day/night length reaches a critical threshold, flight orientation is reversed and emerging adults and their subsequent offspring fly southwards to rejoin the southern part of the species' distribution range in autumn (e.g. Baguette, Stevens & Clobert, 2014; Chapman *et al.*, 2015). Such large-scale, oriented and multi-generational movements occur also in the southern hemisphere worldwide, with inverse seasonality and flight directions. This pattern, involving millions of butterflies and moths (e.g. Chapman *et al.*, 2015), gives the impression of large-scale movements comparable to enormous caribou or wildebeest herds migration. Although here gene flow is at the scale of regions or continents (Baguette *et al.*, 2014), at the individual level, there are no significant differences between this behaviour of semelparous organisms (which has been referred to as migration) and the teleological definition of dispersal (movements potentially leading to gene flow; Ronce, 2007).

Nomadic species also present a particular challenge in terms of definitions for their long-distance movements as they constantly move through the landscape in an unpredictable manner which is not repeated across time. It is broadly accepted that nomadism is an adaptation to environments with low productivity and a resource distribution which is highly variable and unpredictable in space and time (Mueller & Fagan, 2008; Jonzén *et al.*, 2011). However, it is not clear whether nomadism should be considered as a form of non-seasonal and undirected migration or a form of recurring breeding dispersal. In species/clades where individuals express several types of movements (Löfgren, Hörnfeldt & Carlsson, 1986; Korpimäki, Lagerström & Saurola, 1987; Mueller *et al.*, 2011), nomads may move over an extremely large spatial scale (Mueller *et al.*, 2011), and these movements appear largely driven by temporal variation in resources (Jonzén *et al.*, 2011). However, nomadic individuals move in response to both environmental and social cues, most of which are still poorly identified. These cues are likely more labile than the recurrent cues used by seasonal migrants, so that a nomadic strategy is more plastic and less endogenously controlled (Jonzén *et al.*, 2011), hence more akin to dispersal (Bennetts & Kitchens, 2000; Schwarzkopf & Alford, 2002). Moreover, nomadic movements may involve either solitary individuals or groups (see Section IV.1). The main difference between the nomadic movements of groups and the breeding dispersal movements that occur in sedentary species is that the whole group or population moves together in space (Roshier & Reid, 2003). Although virtually nothing is known about dispersal among social groups in nomadic species, both nomadism and dispersal always lead to some kind of gene flow, while migration does not necessarily do so.

(2) An evolutionary view of long-distance movements and their synchronization

Dispersal and seasonal migration have completely different ecological functions and evolutionary dynamics, with different ultimate and proximate causation. Indeed, although certain ecological factors may be implicated in both migration and dispersal (i.e. food availability, predation risk), these two types of movement have evolved in response to different selection pressures: dispersal has evolved as a response to multiple drivers, notably kin interactions and inbreeding avoidance, intra-specific competition and environmental stochasticity, whereas migration has evolved in highly seasonal environments in response to large-scale and predictable spatio-temporal variation in ecological conditions. As a consequence, individuals repeat migratory movements every year, while dispersal movements occur occasionally over an individual's lifetime (except for nomadism). Therefore, even when a given ecological factor drives the evolution of both migration and dispersal, the intensity and nature of the selection pressure may often differ. For instance, the cumulative lifetime risk of predation should be higher for migrating than for dispersing individuals and may therefore drive stronger selection for group movements. From a proximate point of view, migratory strategies are believed to be mostly genetically determined and fixed (i.e. directionality, timing), whereas dispersal was traditionally considered as environmentally determined and plastic until recent demonstrations of (*i*) significant heritability in this behaviour (Zera & Brisson, 2012) and (*ii*) the existence of dispersal syndromes, i.e. suites of traits associated with different dispersal strategies, both among (Stevens *et al.*, 2014) and within species (Ronce & Clobert, 2012).

However, despite these differences, the evolution of dispersal and migration may be inter-connected (Salewski & Bruderer, 2007), at least in part because they depend on the same locomotory systems. First, it has been hypothesized that dispersal was a precursor to the evolution of migration (Salewski & Bruderer, 2007). When a species expands its distribution through dispersal, it may colonize habitats where conditions are unsuitable for some parts of the year. This may cause individuals to migrate back to the natal range after breeding in order to survive, returning only at the next breeding season. For example, in house finches (*Carpodacus mexicanus*) introduced to the north-eastern USA, the proportion of migrants increased after introduction as the population extended its range (Able & Belthoff, 1998; Salewski & Bruderer, 2007). On the other hand, asynchrony in migration may lead to some degree of gene flow (and so be considered as a form of dispersal) in certain circumstances, and has even been hypothesized to be a driver of speciation. For example, in waterfowl, males may migrate to the breeding range of their female partners which can be spatially distinct from their original breeding range (Rodway, 2007), leading to gene flow. More generally, migrants may travel to a separate breeding range because of navigational error and low homing precision. For example, although homing precision in salmonids is generally higher than in non-salmonid species (Lucas *et al.*, 2001), a proportion of salmon fail to return to their natal rivers and are recaptured in nearby rivers, potentially driving the colonization of new habitats (Quinn, 1993; Lohmann, Putman & Lohmann, 2008).

From our review, it appears that spatial and temporal synchronization during the three phases of dispersal (departure, transience and settlement) is not very widespread across taxa, and that synchronization during transience and settlement mostly occurs when departure is also synchronized. By contrast, seasonal migration is one of the most striking examples of synchronized behaviour in the animal world, although the degree of synchronization may vary across the different migration phases. Nomadism is particularly interesting in this respect, as it comprises both coordinated and uncoordinated movements, with differences among and within species. Nomadic individuals move across the landscape along routes that can vary among individuals (type I nomadism; Mueller & Fagan, 2008) or among years (type II nomadism; Mueller & Fagan, 2008), depending on whether individuals are moving among multiple resource-rich patches, or tracking a few resource patches. While the first type likely precludes coordinated movements among individuals (e.g. Bennetts & Kitchens, 2000; Schwarzkopf & Alford, 2002; Mueller *et al.*, 2011), the second type often leads to movement synchronization (Dean, 1997; Dorfman & Kingsford, 2001; McClure, Ralph & Despland, 2011; Pedler, Ribot & Bennett, 2014). For example, to track unpredictable broad-scale variation in resources, nomadic Mongolian gazelles (*Procapra gutturosa*) move independently and in an uncoordinated manner (Mueller *et al.*, 2011). On the contrary, in arid and semi-arid environments in South Africa and Australia, nomadic bird species often move in groups of variable size (Dean, 1997; Pedler *et al.*, 2014), while in the nomadic caterpillar (*Malacosoma disstria*) movements are highly synchronized, with the entire colony travelling together (McClure *et al.*, 2011). This suggests that movement synchronization may mainly emerge in response to environmental drivers such as resource dynamics. However, collective movement and collective decision making (e.g. integration of information collected by many individuals) could also procure advantages for detecting and responding to highly unpredictable and rapidly changing pulses of resource availability (Jonzén *et al.*, 2011). For example, from the foraging success of other individuals, conspecifics can obtain information about habitat suitability (Valone, 1989), or find suitable travelling routes (Åkesson & Hedenström, 2007). The so called 'many-wrongs principle' states that if each individual makes their own, error-prone, assessment, but then tends to align with the direction of motion of others, environmental noise can be dampened due to multiple sampling by individuals within a group (Simons, 2004). Groups can also display an awareness of the environment which is not possible at the individual level. When local environment quality decreases, groups can respond to gradients that are impossible for an individual to perceive (Torney, Neufeld & Couzin, 2009).

V. PERSPECTIVES

(1) Why does synchronization in dispersal matter?

There are multiple reasons that warrant spending greater effort on increasing our understanding of synchronized dispersal behaviours, spanning from fundamental ecological and evolutionary theory, through consequences for population dynamics and genetic structure, to applications for better understanding and managing species' responses to environmental change.

First, collective dispersal behaviours are interesting in their own right. While above we have outlined the reasons why we should expect selection to favour collective movements in certain contexts, we still lack a coherent picture of when and how we should expect exceptions to this pattern. This ultimately boils down to understanding the benefits and costs associated with these different types of movements. Hence, we could look at the problem from the opposing perspective, using these exceptions (if they really are exceptions) better to understand the selection pressures acting on dispersal and migration. Moreover, collective dispersal may be an important driver of the evolution of other social behaviours that are difficult to explain such as, for example, altruism (Gardner & West, 2006). Interestingly, understanding collective dispersal may also aid understanding of the evolution of mating systems. For example, inbreeding avoidance is thought to be an important driver of dispersal (Perrin & Mazalov, 2000; Szulkin & Sheldon, 2008). However, from an inclusive fitness point of view, certain levels of inbreeding could be beneficial to a degree that varies between males and females (Kokko & Ots, 2006; Szulkin *et al.*, 2013). The balance between the costs and benefits of inbreeding will influence the cost/benefit balance of dispersing together with relatives or as single individuals (Koykka & Wild, 2015).

Second, collective dispersal has potentially important consequences for the maintenance and structuring of genetic diversity within and among populations (Fix, 2004; Broquet *et al.*, 2013; Yearsley, Viard & Broquet, 2013). Classic population genetic theory considers gene flow and hence dispersal as one of the major forces that reduces genetic diversity between populations and stabilizes allelic frequencies, counteracting micro-evolutionary local adaptation and genetic drift. However, studies focusing on collective dispersal, particularly when involving kin ('kin-structured migration': Rogers, 1987; Fix, 2004), have highlighted how kin dispersing in groups, as they are not a random sample of the source population, can actually increase genetic differentiation between neighbouring populations so that significant local micro-evolutionary adaptation is not necessarily precluded. These effects appear to be more likely in small populations with high dispersal rates. Hence, understanding when collective dispersal occurs and how dispersing groups are structured in terms of inter-individual relatedness is important for the understanding of evolutionary processes and genetic structure across species' ranges. In particular, considering the genetic effects of collective dispersal could be crucial for predicting outcomes in terms of range expansion and/or shift of species, as the colonization front is generally composed of small founder populations that often exhibit high dispersal propensity.

The influence of collective movement on genetic structure and diversity also has important implications for inference regarding the process of dispersal. With a model focusing on neutral dynamics, Yearsley *et al.* (2013) showed that collective dispersal reduces genetic mixing between populations, which decreases expected coalescence times and increases among-population differentiation (e.g. F_{ST}, the genetic population differentiation index). This will affect estimates of dispersal rates and/or dispersal kernels inferred from genetic data. For example, high F_{ST} values, which would be generally interpreted as a sign of low dispersal rates, could in fact be the result of high rates of collective dispersal (Yearsley *et al.*, 2013).

Third, collective dispersal can play an important role in metapopulation and range dynamics. For example, perhaps intuitively, collective dispersal has been shown to be beneficial for metapopulation persistence in the presence of strong Allee effects (Fernandez *et al.*, 2012). In a simulation study on the dynamics of species invasion, Fogarty *et al.* (2011) included a sociability trait and found that a population consisting of social and asocial strategies had a higher chance of survival or expanding its range relative to a monomorphic population for either strategy. Hence, in some species, heterogeneity in personality, which is potentially linked to the propensity for collective movements (Johnstone & Manica, 2011), might be important for shaping the dynamics of species range expansions. Intriguingly, we may speculate as to whether recent environmental changes that force species to shift their ranges rapidly might exert positive selection pressure not only for dispersal propensity to increase, but also for dispersal behaviours to become more synchronized.

Because of these potentially far-reaching consequences of collective dispersal for both ecological and evolutionary processes, it seems clear that we should consider synchronization of dispersal as we build increasingly sophisticated models for predicting species' responses to environmental changes and for providing management recommendations, whether for conservation or containment of invasive species. However, before adding this complexity to predictive models, it is crucial that we first invest time and resources for developing underpinning theory and collecting high-quality empirical data.

(2) Advancing theory on synchronized dispersal

Theory on collective movements of animals and, more broadly, on collective decision making and behaviours, has been gaining momentum over the past decade (Conradt & Roper, 2005; Sumpter, 2010). This field has made exciting progress in advancing our understanding of mechanisms, proximate causes and ultimate evolutionary drivers of collective movements. Work has mainly focused on small spatio-temporal-scale movements such as, for example, foraging, with the exception of some initial work done on migration (Guttal & Couzin, 2010). However, dispersal theory has yet to harness these advances, leaving an almost completely unexplored field of research: when should we expect individuals to take collective dispersal decisions and synchronize their dispersal behaviours? Below, we briefly highlight the main theoretical concepts on collective movements/decision making of animals and suggest possible ways in which these could be integrated with theory on the evolution of dispersal. Rather than focusing on how animals move together (for a review see Sumpter, 2010), we concentrate on why they do so and why collective movements are expected to emerge from individual behaviours or to evolve as a life-history strategy.

Theory on collective decision making deals with two fundamental points: the acquisition and sharing of information, and the resolution of conflicts of interest between individuals who have to converge towards consensual decisions in order to perform synchronized behaviours. A variety of theoretical models, most of which make use of game theory principles, have been formulated to address both issues and have been recently reviewed by Conradt (2012). Models considering information acquisition often ask which strategies of collective decision making are expected to maximize information accuracy and minimize the time taken to achieve the decision. In other words, given a degree of information uncertainty, is it advantageous to take decisions as a group and, if so, which strategies of group decision making should we expect to evolve? Models include: (*i*) quorum responses (Sumpter & Pratt, 2009), which lead to a more accurate collective decision compared to a solitary decision, but at the cost of slowing the decision process; (*ii*) leadership models (Couzin *et al.*, 2005), which have shown that once a certain number of individuals hold information, other individuals can benefit from following the informed individuals without themselves investing in information acquisition; (*iii*) independence–interdependence models (List, Elsholtz & Seeley, 2009), which have shown how the group can benefit from the pooling of information acquired by multiple independent individuals; (*iv*) models of social parasitism, such as the producer–scroungers game (Sumpter, 2010), where some individuals invest in information acquisition (for example, food sources), while others exploit that information.

Conflict models deal with situations where the balance between costs and benefits of achieving a collective decision, and hence performing a collective behaviour, vary among individuals (Conradt & Roper, 2005; Conradt, 2012). Typically, these models consider cases where the optimal timing for initiating a particular behaviour, or the optimal destination of a particular movement, differs among individuals or among sub-groups of individuals (e.g. ages, sexes, physiological states). The magnitude and distribution of consensus costs among individuals are particularly important (i.e. the cost of taking consensual decisions and performing collective behaviours) relative to the benefits. Interestingly, it has been shown that we should expect collective decisions to emerge more often for the initiation (timing) of a particular movement, with predictions about leadership involving needs, physiological status or personalities (Bazazi *et al.*, 2011; Johnstone & Manica, 2011), than for the movement destination (space). In the latter case, when consensus costs are high, we should expect either dictatorial or solitary decision making to evolve (Conradt & Roper, 2009). As Sumpter (2010) pointed out, collective behaviours, specifically movements in our case, can ultimately be classified as coordinated and cooperative. Here, the assumption is that individuals move because it is beneficial for them to do so, but coordination can emerge because a number of individuals use the same environmental cues, or because some animals copy more-informed individuals. By contrast, cooperation should evolve as a result of the benefits of moving as a group outweighing the costs. Game theoretic models that seek to explain the evolution of cooperative movement/behaviours include social parasitism, mutualism, synergism, repeated interactions and altruism (Sumpter, 2010).

These concepts have been applied by Guttal & Couzin (2010) in their individual-based, spatially explicit evolutionary model for the evolution of collective migration. In this model, there are two evolving traits that determine individual fitness by accruing the costs and benefits associated with migration: 'gradient detection ability' and 'sociality'. The 'gradient detection ability' trait determines an individual's ability to collect information about the environmental gradient it needs to follow to perform efficient migration. The 'sociality' trait determines the individual's tendency to be attracted to, and follow, other individuals. Both traits carry costs which increase monotonically with the trait values, and individuals reproduce with a probability that is proportional to the net cost–benefit balance determined by their strategy. Depending on the conditions and on the magnitude of, and balance between, the costs of the two traits, different strategies are predicted to evolve: residency (non-migration), solitary migration, collective migration in cohesive groups and collective migration resulting from fission–fusion dynamics initiated by a few leaders (Guttal & Couzin, 2011). Collective migration evolves under a large range of conditions associated with intermediate costs of sociality and gradient detection ability, and also at very low population densities where individuals would be expected to interact only rarely. Interestingly, when collective migration evolves, it includes two co-existing frequency-dependent strategies: 'leaders' who have high gradient-detection ability, but low sociality, and 'social individuals' who have low or no gradient-detection ability, but a high propensity for social interactions. Furthermore, at high levels of habitat fragmentation 'leader' strategies disappear, causing migration to be lost and, making it extremely difficult for a migratory strategy to reappear, even following habitat restoration.

The commonalities between the body of theory briefly outlined above and dispersal behaviour are remarkable but, from a theoretical point of view, still massively under-explored. Throughout the previous sections, we have highlighted the recent interest in 'informed dispersal' (Clobert *et al.*, 2009) and provided examples on how individuals rely on environmental and social cues to take decisions at each stage of the dispersal process

(Doligez *et al.*, 2002, 2003; Cote & Clobert, 2007*a*, 2010; Boulinier *et al.*, 2008; De Meester & Bonte, 2010). From the theoretical side, much work has been done on the evolution of density-dependent dispersal decisions, mainly focusing on emigration, where individuals' decisions on departure and/or settlement depend on information about the local density of conspecifics (Travis, Murrell & Dytham, 1999; Travis *et al.*, 2009; Hovestadt, Kubisch & Poethke, 2010; Poethke, Gros & Hovestadt, 2011). However, relatively little attention has been paid so far to the role of information uncertainty (Schjorring, 2002; Bocedi, Heinonen & Travis, 2012). Importantly, very little theory has been developed on how we should expect individuals to make use of information possessed by conspecifics at different stages of dispersal (Clobert *et al.*, 2009), whether and how we should expect individuals to follow conspecifics, maybe evolving a form of social parasitism, and whether this could result in collective/synchronized movement behaviours at any of the three stages of dispersal. The model of Guttal & Couzin (2010, 2011) provides an excellent example of how the fields of collective movement, migration and evolutionary modelling can be integrated to obtain insight on the evolutionary dynamics of solitary *versus* collective large-scale movements. Importantly, it also provides a first example of how this type of model could be used to understand if and how individual movement strategies matter for predicting a species' response to environmental change and, in turn, how environmental change may impact these strategies.

Conflict models are particularly relevant for dispersal. In fact, much more so than for migration, dispersing individuals often have contrasting interests with regards to when and where to disperse. These conflicts arise as a consequence of the ultimate causes of dispersal. Individuals dispersing to avoid kin competition might not want to settle together and compete with their kin for resources, hence, the decisions regarding whether or not to emigrate and where to settle should differ among kin. Similarly, if dispersal evolved as an inbreeding-avoidance strategy, relatives of the opposite sex may have conflicting interests as to whether or not to disperse, as well as to when and where to disperse, leading, for example, to sex-biased dispersal. Both kin competition and inbreeding avoidance can exert contrasting selective pressures on different individuals, as the distribution of relatives in a population is likely to vary in time and space, and so be specific for a given individual. However, if dispersal evolved as a strategy to escape habitat deterioration, individuals might benefit from moving at the same time, pooling collective effort to find a suitable new habitat patch. Similarly, if populations are subject to Allee effects, moving together could facilitate group settlement, thereby mitigating the risk of reduced fitness due to low conspecific density. The prediction that collective decisions are expected to evolve more often for movement initiation than for movement destination seems to support the observation that collective decisions appear to be more prevalent during emigration than during settlement (see Section II). However, the above prediction was not developed from models looking explicitly at dispersal. In reality, dispersal behaviours are likely to evolve in response to multiple drivers (Clobert *et al.*, 2012), making it challenging to predict whether or not group dispersal should be expected. Importantly, conflict models that wish to tackle these issues should incorporate these multiple drivers as sources of conflicting interests among individuals.

Interestingly, the field of collective animal behaviour and decision making has identified one of its future challenges as understanding how the outcome of evolutionary games for conflict decisions is influenced by information uncertainty (Conradt, 2012). In parallel, dispersal theory needs to move to the next level, integrating individual use of multiple sources of information with the multiple drivers of dispersal (Clobert *et al.*, 2009). It is therefore clear that a tighter interaction between the two fields could lead to mutual progress and aid understanding of when and where we should expect collective dispersal. Theory on synchronized dispersal evolution can further draw from what it is known about the density-dependence of synchronization in migratory behaviours. Partial migration, where only a part of the population migrates, is particularly interesting because it creates opportunity for frequency- and density-dependence of movement tactics. Most drivers of partial migration also depend on density [e.g. five out of eight hypotheses in Chapman *et al.* (2011*a*): competition for resources or breeding opportunities, predation risk and intraspecific niche diversity (Chapman *et al.*, 2011*a*; Avgar *et al.*, 2014)] and so does the frequency of migratory and resident tactics (Kokko, 2011; Mysterud *et al.*, 2011). All the hypotheses that have been put forward to explain partial migration (especially in mammals; Avgar *et al.*, 2014), such as social fences, competition avoidance or predation risk avoidance, are highly sensitive to population density. Indeed, population density modulates the benefits and costs of social grouping and might thus change the frequencies of migratory tactics. For example, a large-scale monitoring of red deer (*Cervus elaphus*) populations in Norway revealed negative density-dependence in the proportion of migrants (Mysterud *et al.*, 2011), which tends to favour the social fence hypothesis rather than competition avoidance. In turn, the frequency of migratory tactics may suddenly alter local population densities. High frequencies of migrants leaving together may push remaining residents to leave afterwards and eventually lead to the migration of the entire population. Population density is also central to many theories on dispersal evolution; however, no theory has looked at the potential effect of strong density-dependence on the synchronization (especially temporal) of dispersal behaviours, or at how temporal synchronization could in turn affect population density, hence feeding back to the optimal dispersal strategy.

(3) Empirical studies: data collection and analysis

The three phases of the dispersal process are rarely all monitored within a given study. For example, researchers commonly observe the timing of dispersal departure (i.e. emigration) and/or settlement (i.e. immigration), whereas transience is almost always neglected. A major reason for this is the practical and technical difficulties of monitoring movements of individuals over large spatial and temporal scales. Without detailed monitoring of a sufficient number of individually recognizable animals across the three movement stages, it is hard to ascertain whether individuals disperse on their own or as a synchronized group. Previously, researchers had to rely on direct observation of individually recognizable animals in areas where observability was high, for example, large ungulates and carnivores in open plains (Holekamp, Boydston & Smale, 2000), and/or repeated capture data of individually marked animals. Alternatively, movement synchrony is sometimes deduced where, following movement, individuals are still associated with known members of their previous social unit, which could imply that they dispersed together (Sharp *et al.*, 2008).

Dispersal studies would clearly benefit from adopting methods routinely used in migration and foraging studies (Lucas *et al.*, 2001). Sophisticated tracking devices have become widely available, making it possible to track individuals accurately and precisely over large distances (Nathan *et al.*, 2003). This provides a promising avenue for obtaining information on movement synchrony during dispersal. Simultaneous global positioning system (GPS) tracking of individuals may reveal unexpected social grouping or synchronized dispersal events (Lührs & Kappeler, 2013), although this does not provide information on the associated social context. Indeed, spatial proximity does not necessarily imply coordinated behaviour, although it is reasonable to assume that physical contact should increase as the frequency of close proximity events between pairs of individuals increases. Nonetheless, the frequency of interactions among individuals is vital information for understanding the importance of the social context of dispersal (Prange *et al.*, 2006). Combining telemetry data with information on social interactions is likely to further improve our understanding of the mechanisms and drivers behind the sociality of large-scale movement.

Within the past decade, advances in technology have led to the development of proximity loggers which can provide information on intra-specific interactions indexed by the distance between individuals. Proximity loggers are electronic devices that both emit a unique electronic signal and continuously monitor and record the time and duration of signals emitted by other loggers (Prange *et al.*, 2006), enabling the detection of proximity between two monitored individuals. One major advantage is that a threshold detection distance can be defined, ranging from <1 to 100 m for logging encounters, with distance errors not exceeding 3 m (Cross *et al.*, 2012). This system was primarily developed to study patterns of space use among individuals (Atwood & Weeks, 2003), or location of predatory kills (Tambling & Belton, 2009), but is increasingly used to measure and model contact rates for questions of disease transmission (Hamede *et al.*, 2009), or group membership (Schauber, Storm & Nielsen, 2007). Because it provides continuous, individual-based, contact data without requiring direct observation (Hamede *et al.*, 2009), this technology has tremendous potential for understanding the sociality of dispersal. Currently, the weight and power autonomy significantly limit the applications of these systems, although some recent studies on birds have been successful. For example, miniature proximity loggers have been used on Caledonian crow (*Corvus moneduloides*) to establish a near real-time monitoring of association patterns (Rutz & Troscianko, 2013). However, the use of proximity as a measure of inter-individual interaction still does not provide any information regarding the type and duration of contact. Animal-borne video and environmental data recorders (AVED) could provide information on the type of interaction (i.e. the behaviour of the performer, but also the response of the receiver) in terms of social interaction during movement stages, as well as on environmental conditions (Moll *et al.*, 2007). AVEDs have been used to study feeding habits (Newmaster *et al.*, 2013), the use of tools (Rutz *et al.*, 2007), disease transmission (Lavelle *et al.*, 2012), and predation (Loyd *et al.*, 2013). Further miniaturization (Rutz & Troscianko, 2013) and gains in energy autonomy will increase the future applicability of this technology to a variety of model systems. Coupling proximity loggers with miniature video cameras that are activated when the individual is within a certain distance of a congener could be an energy-efficient way of recording sociality during movement (Rutz & Troscianko, 2013).

VI. CONCLUSIONS

(1) Dispersal and migration are two conspicuous and superficially similar large-scale movement behaviours. However, seasonal migrants are often thought to move together through time and space in a synchronized fashion, while dispersers are believed to be solitary individuals.

(2) Our literature review shows that natal and breeding dispersal movements appear, for the most part, to involve solitary animals. While it appears that temporal and/or spatial synchronization is less unusual than previously thought, the vast majority of published examples clearly concern semelparous and/or cooperative species. By contrast, migratory movements are generally synchronized in time and space within groups of individuals, but there are non-trivial levels of inter-individual variation in behavioural tactics.

(3) The contrast in behavioural synchronization between dispersal and migration may derive from differences in the selection pressures that drive their respective evolution. Indeed, although certain ecological factors may be implicated in both migration and dispersal (i.e. food availability, predation risk), dispersal has evolved as a response to multiple drivers, notably kin interactions and inbreeding avoidance, intra-specific competition and environmental stochasticity, whereas migration has evolved

in highly seasonal environments in response to large-scale spatio-temporal variation in ecological conditions.

(4) Although collective dispersal and solitary migration are seemingly rare, we still lack enough information to rule these processes out as important components of some species eco-evolutionary biology. Crucially, to date, there is hardly any theory developed for collective dispersal: when should we expect to see it, why and how? Progress made on the theory of collective animal movement, particularly regarding foraging, dispersal and, to a lesser extent, migration, offers a promising way to move dispersal theory forward, especially with regard to the use of social information by dispersing individuals and behavioural synchronization.

(5) Understanding the occurrence and mechanisms of these collective behaviours can help us to understand better the selection pressures acting on both dispersal and migration. Furthermore, collective dispersal may have underappreciated and important consequences for species' eco-evolutionary dynamics, affecting the evolution of other behaviours such as mating systems and altruism, for the maintenance and structuring of genetic diversity within and among populations, and for metapopulation dynamics and range expansion. In particular, we still lack a coherent picture of the role played by collective dispersal and of its possible evolution given the novel selection pressures that currently prevail due to rapid global change.

VII. ACKNOWLEDGEMENTS

This work was initiated at a workshop within the 'Movement And Dispersal (MAD)' conference held in Aberdeen, 2013. We thank Tal Avgar, Scott Burgess and two anonymous reviewers for helpful comments on previous versions of this manuscript. This work was based in the Laboratoire Evolution et Diversité Biologique (CNRS, UPS, UMR 5174), and in the Station d'Ecologie Expérimentale du CNRS à Moulis (CNRS USR 2936) that are part of the Laboratoire d'Excellence (LABEX) 'TULIP' (ANR-10-LABX-41 ; ANR-11-IDEX-0002-02) and in the CEFS laboratory, INRA (Toulouse). J.C. was supported by an ANR-12-JSV7-0004-01 and by the ERA-Net BiodivERsA, with the national funder ONEMA, part of the 2012-2013 BiodivERsA call for research proposals. A.J.M.H. and M.B. were supported by the 'INDHET'ANR grant ANR-12 -BSV7-0023-02. H.C.W. thanks the Finnish Doctoral Program in Computational Sciences (FICS) and the Academy of Finland for financial support.

VIII. REFERENCES

References marked with asterisk have been cited within Appendix S1.

Able, K. P. & Belthoff, J. R. (1998). Rapid 'evolution' of migratory behaviour in the introduced house finch of eastern North America. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **265**, 2063–2071.

Aguirre, J. D., Miller, S. H., Morgan, S. G. & Marshall, D. J. (2013). Relatedness affects the density, distribution and phenotype of colonisers in four sessile marine invertebrates. *Oikos* **122**, 881–888.

Åkesson, S. & Hedenström, A. (2007). How migrants get there: migratory performance and orientation. *Bioscience* **57**, 123–133.

Alerstam, T., Hedenstrom, A. & Akesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos* **103**, 247–260.

Alino, P. M. & Coll, J. C. (1989). Observations of the synchronized mass spawning and post settlement activity of octocorals on the Great Barrier Reef, Australia: biological aspects. *Bulletin of Marine Science* **45**, 697–707.

Allen, C. R. & Saunders, D. A. (2002). Variability between scales: predictors of nomadism in birds of an Australian mediterranean-climate ecosystem. *Ecosystems* **5**, 348–359.

Andersson, M. (1980). Nomadism and site tenacity as alternative reproductive tactics in birds. *Journal of Animal Ecology*, **49**(1), 175–184.

Atwood, T. C. & Weeks, H. P. Jr. (2003). Spatial home-range overlap and temporal interaction in eastern coyotes: the influence of pair types and fragmentation. *Canadian Journal of Zoology* **81**, 1589–1597.

Avgar, T., Street, G. & Fryxell, J. M. (2014). On the adaptive benefits of mammal migration. *Canadian Journal of Zoology* **92**, 481–490.

*Aviles, L. (2000). Nomadic behaviour and colony fission in a cooperative spider: life history evolution at the level of the colony? *Biological Journal of the Linnean Society* **70**, 325–339.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M. & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews* **88**, 310–326.

Baguette, M., Stevens, V. M. & Clobert, J. (2014). The pros and cons of applying the movement ecology paradigm for studying animal dispersal. *Movement Ecology* **2**, 1–13.

Baker, R. (1978). *Evolutionary Ecology of Animal Migration*. Holmes & Meier Publishers, New York.

Battley, P. F. (2006). Consistent annual schedules in a migratory shorebird. *Biology Letters* **2**, 517–520.

Bauer, S. & Hoye, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* **344**, 1242552.

Bauer, S. & Klaassen, M. (2013). Mechanistic models of animal migration behaviour their diversity, structure and use. *Journal of Animal Ecology* **82**, 498–508.

*Bayart, F. & Simmen, B. (2005). Demography, range use, and behavior in black lemurs (*Eulemur macaco macaco*) at Ampasikely, northwest Madagascar. *American Journal of Primatology* **67**, 299–312.

Bazazi, S., Romanczuk, P., Thomas, S., Schimansky-Geier, L., Hale, J. J., Miller, G. A., Sword, G. A., Simpson, S. J. & Couzin, I. D. (2011). Nutritional state and collective motion: from individuals to mass migration. *Proceedings of the Royal Society B-Biological Sciences* **278**, 356–363.

Bennetts, R. E. & Kitchens, W. M. (2000). Factors influencing movement probabilities of a nomadic food specialist: proximate foraging benefits or ultimate gains from exploration? *Oikos* **91**, 459–467.

Ben-Tzvi, O., Abelson, A., Gaines, S. D., Bernardi, G., Beldade, R., Sheehy, M. S., Paradis, G. L. & Kiflawi, M. (2012). Evidence for cohesive dispersal in the sea. *PLoS One* **7**, e42672.

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.

Bergmüller, R., Heg, D., Peer, K. & Taborsky, M. (2005). Extended safe havens and between-group dispersal of helpers in a cooperatively breeding cichlid. *Behaviour* **142**, 1643–1667.

Bernardi, G., Beldade, R., Holbrook, S. J. & Schmitt, R. J. (2012). Full-sibs in cohorts of newly settled coral reef fishes. *PLoS One* **7**, e44953.

Bestion, E., Clobert, J. & Cote, J. (2015). Dispersal response to climate change: scaling down to intraspecific variation. *Ecology Letters* **18**, 1226–1233.

Bestion, E., Teyssier, A., Aubret, F., Clobert, J. & Cote, J. (2014). Maternal exposure to predator scents: offspring phenotypic adjustment and dispersal. *Proceedings of the Royal Society B: Biological Sciences* **281**(1792) (doi: 10.1098/rspb.2014.0701.

Bety, J., Giroux, J. F. & Gauthier, G. (2004). Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). *Behavioral Ecology and Sociobiology* **57**, 1–8.

Binder, T. R., Cooke, S. J. & Hinch, S. G. (2011). The biology of fish migration. In *Encyclopedia of Fish Physiology: From Genome to Environment*, pp. 1921–1927. Academic Press, San Diego.

Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., Van Moorter, B., Mysterud, A., Gaillard, A. E. J.-M. & McPeek, E. M. A. (2012). A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? *The American Naturalist* **180**, 407–424.

Bitume, E. V., Bonte, D., Ronce, O., Bach, F., Flaven, E., Olivieri, I. & Nieberding, C. M. (2013). Density and genetic relatedness increase dispersal distance in a subsocial organism. *Ecology Letters* **16**, 430–437.

Bleich, V. C. & Pierce, B. M. (2001). Accidental mass mortality of migrating mule deer. *Western North American Naturalist* **61**, 124–125.

Bocedi, G., Heinonen, J. & Travis, J. M. J. (2012). Uncertainty and the role of information acquisition in the evolution of context-dependent emigration. *The American Naturalist* **179**, 606–620.

*Boinski, S. (2005). Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii, S. boliviensis and S. sciureus*): III. Cognition. *Behaviour* **142**, 679–699.

Bonhomme, F. & Planes, S. (2000). Some evolutionary arguments about what maintains the pelagic interval in reef fishes. *Environmental Biology of Fishes* **59**, 365–383.

Bonte, D., Travis, J. M. J., De Clercq, N., Zwertvaegher, I. & Lens, L. (2008). Thermal conditions during juvenile development affect adult dispersal in a spider. *Proceedings of the National Academy of Sciences* **105**, 17000–17005.

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barton, K., *et al.* (2012). Costs of dispersal. *Biological Reviews* **87**, 290–312.

Börger, L., Matthiopoulos, J., Holdo, R. M., Morales, J. M., Couzin, I., McCauley, E., Milner-Gulland, E. J., Fryxell, J. M. & Sinclair, A. R. E. (2011). Migration quantified: constructing models and linking them with data. In *Animal Migration—a Synthesis*, pp. 111–128. Oxford University Press, Oxford.

Boulinier, T., McCoy, K. D., Yoccoz, N. G., Gasparini, J. & Tveraa, T. (2008). Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours. *Biology Letters* **4**, 538–540.

Bowler, D. E. & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* **80**, 205–225.

Boyle, W. A. & Conway, C. J. (2007). Why migrate? A test of the evolutionary precursor hypothesis. *The American Naturalist* **169**, 344–359.

Braendle, C., Davis, G. K., Brisson, J. A. & Stern, D. L. (2006). Wing dimorphism in aphids. *Heredity* **97**, 192–199.

Breitburg, D. L. (1989). Demersal schooling prior to settlement by larvae of the naked goby. *Environmental Biology of Fishes* **26**, 97–103.

Brodersen, J., Nilsson, P. A., Chapman, B. B., Skov, C., Hansson, L.-A. & Brönmark, C. (2012). Variable individual consistency in timing and destination of winter migrating fish. *Biology Letters* **8**, 21–23.

Brönmark, C., Skov, C., Brodersen, J., Nilsson, P. A. & Hansson, L.-A. (2008). Seasonal migration determined by a trade-off between predator avoidance and growth. *PLoS One* **3**, e1957.

Broquet, T., Viard, F. & Yearsley, J. M. (2013). Genetic drift and collective dispersal can result in chaotic genetic patchiness. *Evolution* **67**, 1660–1675.

*Buhl, J., Sword, G. A., Clissold, F. J. & Simpson, S. J. (2011). Group structure in locust migratory bands. *Behavioral Ecology and Sociobiology* **65**, 265–273.

Burgess, S. C., Baskett, M. L., Grosberg, R. K., Morgan, S. G. & Strathmann, R. R. (2016). When is dispersal for dispersal? Unifying marine and terrestrial perspectives. *Biological Reviews* **91**, 867–882.

Burghardt, G. M., Greene, H. W. & Rand, A. S. (1977). Social behavior in hatchling green iguanas: life at a reptile rookery. *Science* **195**, 689–691.

Byers, J. E. (2000). Effects of body size and resource availability on dispersal in a native and a non-native estuarine snail. *Journal of Experimental Marine Biology and Ecology* **248**, 133–150.

Chapman, M. G. (1986). Assessment of some controls in experimental transplants of intertidal gastropods. *Journal of Experimental Marine Biology and Ecology* **103**, 181–201.

Chapman, B. B., Brönmark, C., Nilsson, J.-Å. & Hansson, L.-A. (2011*a*). The ecology and evolution of partial migration. *Oikos* **120**, 1764–1775.

Chapman, B. B., Hulthén, K., Blomqvist, D. R., Hansson, L.-A., Nilsson, J.-Å., Brodersen, J., Anders Nilsson, P., Skov, C. & Brönmark, C. (2011*b*). To boldly go: individual differences in boldness influence migratory tendency. *Ecology Letters* **14**, 871–876.

Chapman, J. W., Reynolds, D. R. & Wilson, K. (2015). Long-range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences. *Ecology Letters* **18**, 287–302.

Chesser, R. T. & Levey, D. J. (1998). Austral migrants and the evolution of migration in new world birds: diet, habitat, and migration revisited. *The American Naturalist* **152**, 311–319.

Clobert, J., Baguette, M., Benton, T. G., Bullock, J. M. & Ducatez, S. (2012). *Dispersal. Ecology and Evolution*. Oxford University Press, New York.

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.

Clotuche, G., Mailleux, A.-C., Astudillo Fernández, A., Deneubourg, J.-L., Detrain, C. & Hance, T. (2011). The formation of collective silk balls in the spider mite *Tetranychus urticae* Koch. *PLoS One* **6**, e18854.

Clotuche, G., Turlure, C., Mailleux, A.-C., Detrain, C. & Hance, T. (2013). Should I lay or should I wait? Egg-laying in the two-spotted spider mite *Tetranychus urticae* Koch. *Behavioural Processes* **92**, 24–30.

Cockburn, A. (1998). Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics* **29**, 141–177.

*Collevatti, R. G., Souza-Neto, A. C., Silva, N. J. & Telles, M. P. C. (2013). Kin structure and parallel dispersal in the black-and-gold howler monkey *Alouatta caraya* (Platyrrhini, Atelidae). *Genetics and Molecular Research* **12**, 6018–6031.

Conradt, L. (2012). Models in animal collective decision-making: information uncertainty and conflicting preferences. *Interface Focus* **2**(2) (doi: 10.1098/rsfs20110090).

Conradt, L. & Roper, T. J. (2005). Consensus decision making in animals. *Trends in Ecology & Evolution* **20**, 449–456.

Conradt, L. & Roper, T. J. (2009). Conflicts of interest and the evolution of decision sharing. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 807–819.

Cote, J., Boudsocq, S. & Clobert, J. (2008). Density, social information, and space use in the common lizard (*Lacerta vivipara*). *Behavioral Ecology* **19**, 163–168.

Cote, J. & Clobert, J. (2007*a*). Social information and emigration: lessons from immigrants. *Ecology Letters* **10**, 411–417.

Cote, J. & Clobert, J. (2007*b*). 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.

Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society, B: Biological Sciences* **365**, 4065–4076.

Cote, J., Clobert, J. & Fitze, P. S. (2007). Mother – offspring competition promotes colonization success. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 9703–9708.

Cote, J., Fogarty, S., Brodin, T., Weinersmith, K. & Sih, A. (2011). Personality-dependent dispersal in the invasive mosquitofish: group composition matters. *Proceedings of the Royal Society B: Biological Sciences* **278**, 1670–1678.

Cote, J., Fogarty, S. & Sih, A. (2012). Individual sociability and choosiness between shoal types. *Animal Behaviour* **83**, 1469–1476.

Cote, J., Fogarty, S., Tymen, B., Sih, A. & Brodin, T. (2013). Personality-dependent dispersal cancelled under predation risk. *Proceedings of the Royal Society B: Biological Sciences*, **280**(1733) (doi: 10.1098/rspb.2013.2349).

Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature* **433**, 513–516.

Craig, A. S., Herman, L. M., Gabriele, C. M. & Pack, A. A. (2003). Migratory timing of humpback whales (*Megaptera novaeangliae*) in the Central North Pacific varies with age, sex and reproductive status. *Behaviour* **140**, 981–1001.

Cross, P. C., Creech, T. G., Ebinger, M. R., Heisey, D. M., Irvine, K. M. & Creel, S. (2012). Wildlife contact analysis: emerging methods, questions, and challenges. *Behavioral Ecology and Sociobiology* **66**, 1437–1447.

Danilkin, A. & Hewison, A. J. M. (1996). *Behavioural Ecology of Siberian and European Roe Deer*. Chapman & Hall, London [etc.].

Dean, W. R. J. (1997). The distribution and biology of nomadic birds in the Karoo, South Africa. *Journal of Biogeography* **24**, 769–779.

Debeffe, L., Focardi, S., Bonenfant, C., Hewison, A. J. M., Morellet, N., Vanpe, C., Heurich, M., Kjellander, P., Linnell, J. D. C., Mysterud, A., Pellerin, M., Sustr, P., Urbano, F. & Cagnacci, F. (2014). A one night stand? Reproductive excursions of female roe deer as a breeding dispersal tactic. *Oecologia* **176**, 431–443.

Debeffe, L., Morellet, N., Cargnelutti, B., Lourtet, B., Bon, R., Gaillard, J.-M. & Hewison, A. J. M. (2012). Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. *Journal of Animal Ecology* **81**, 1327.

De Meester, N. & Bonte, D. (2010). Information use and density-dependent emigration in an agrobiont spider. *Behavioral Ecology* **21**, 992–998.

Dingle, H. (2014). *Migration: The Biology of Life on the Move*. Oxford University Press, Oxford.

Dingle, H. & Drake, V. A. (2007). What is migration? *Bioscience* **57**, 113–121.

Doligez, B., Cadet, C., Danchin, E. & Boulinier, T. (2003). When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour* **66**, 973–988.

Doligez, B., Danchin, E. & Clobert, J. (2002). Public information and breeding habitat in a wild bird population. *Science* **297**, 1168–1170.

van Dongen, W. F. D., van Wagner, R. H., Moodley, Y. & Schaedelin, F. C. (2014). Sex biases in kin shoaling and dispersal in a cichlid fish. *Oecologia* **176**, 965–974.

Dorfman, E. J. & Kingsford, R. T. (2001). Scale-dependent patterns of abundance and habitat use by cormorants in arid Australia and the importance of nomadism. *Journal of Arid Environments* **49**, 677–694.

Duriez, O., Bauer, S., Destin, A., Madsen, J., Nolet, B. A., Stillman, R. A. & Klaassen, M. (2009). What decision rules might pink-footed geese use to depart on migration? An individual-based model. *Behavioral Ecology* **20**, 560–569.

Erlandsson, J. & Kostylev, V. (1995). Trail following, speed and fractal dimension of movement in a marine prosobranch, *Littorina littorea*, during a mating and a non-mating season. *Marine Biology* **122**, 87–94.

*Fedigan, L. M. & Jack, K. M. (2004). The demographic and reproductive context of male replacements in *Cebus capucinus*. *Behaviour* **141**, 755–775.

FERNANDEZ, A. A., HANCE, T. & DENEUBOURG, J. L. (2012). Interplay between Allee effects and collective movement in metapopulations. *Oikos* **121**, 813–822.

FIX, A. G. (2004). Kin-structured migration: causes and consequences. *American Journal of Human Biology* **16**, 387–394.

FOGARTY, S., COTE, J. & SIH, A. (2011). Social personality polymorphism and the spread of invasive species: a model. *The American Naturalist* **177**, 273–287.

FRAGOSO, J. M. V. (1997). Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *Journal of Ecology* **85**, 519–529.

FRONHOFER, E. A., KLECKA, J., MELIÁN, C. J. & ALTERMATT, F. (2015*a*). Condition-dependent movement and dispersal in experimental metacommunities. *Ecology Letters* **18**, 954–963.

FRONHOFER, E. A., KROPF, T. & ALTERMATT, F. (2015*b*). Density-dependent movement and the consequences of the Allee effect in the model organism *Tetrahymena*. *Journal of Animal Ecology* **84**, 712–722.

FRYXELL, J. M., MOSSER, A., SINCLAIR, A. R. E. & PACKER, C. (2007). Group formation stabilizes predator-prey dynamics. *Nature* **449**, 1041–1043.

GAILLARD, J. M., ANDERSEN, R., DELORME, D. & LINNELL, J. D. C. (1998). Family effects on growth and survival of juvenile roe deer. *Ecology* **79**, 2878–2889.

GARANT, D., KRUUK, L. E. B., WILKIN, T. A., MCCLEERY, R. H. & SHELDON, B. C. (2005). Evolution driven by differential dispersal within a wild bird population. *Nature* **433**, 60–65.

*GARDNER, A., ARCE, A. & ALPEDRINHA, J. (2009). Budding dispersal and the sex ratio. *Journal of Evolutionary Biology* **22**, 1036–1045.

GARDNER, A. & WEST, S. A. (2006). Demography, altruism, and the benefits of budding. *Journal of Evolutionary Biology* **19**, 1707–1716.

GAUTIER, P., OLGUN, K., UZUM, N. & MIAUD, C. (2006). Gregarious behaviour in a salamander: attraction to conspecific chemical cues in burrow choice. *Behavioral Ecology and Sociobiology* **59**, 836–841.

GILLIAM, J. F. & FRASER, D. F. (2001). Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. *Ecology* **82**, 258–273.

GRAYSON, K. L. & WILBUR, H. M. (2009). Sex- and context-dependent migration in a pond-breeding amphibian. *Ecology* **90**, 306–312.

*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.

GRISWOLD, C. K., TAYLOR, C. M. & NORRIS, D. R. (2011). The equilibrium population size of a partially migratory population and its response to environmental change. *Oikos* **120**, 1847–1859.

GROSBERG, R. K. & QUINN, J. F. (1986). The genetic control and consequences of kin recognition by the larvae of a colonial marine invertebrate. *Nature* **322**, 456–459.

GSCHWENG, M., KALKO, E. K. V., QUERNER, U., FIEDLER, W. & BERTHOLD, P. (2008). All across Africa: highly individual migration routes of Eleonora's falcon. *Proceedings of the Royal Society of London B: Biological Sciences* **275**, 2887–2896.

GUTTAL, V. & COUZIN, I. D. (2010). Social interactions, information use, and the evolution of collective migration. *Proceedings of the National Academy of Sciences* **107**, 16172–16177.

GUTTAL, V. & COUZIN, I. D. (2011). Leadership, collective motion and the evolution of migratory strategies. *Communicative & Integrative Biology* **4**, 294–298.

*GUTTAL, V., ROMANCZUK, P., SIMPSON, S. J., SWORD, G. A. & COUZIN, I. D. (2012). Cannibalism can drive the evolution of behavioural phase polyphenism in locusts. *Ecology Letters* **15**, 1158–1166.

HAKKARAINEN, H., ILMONEN, P., KOIVUNEN, V. & KORPIMÄKI, E. (2001). Experimental increase of predation risk induces breeding dispersal of Tengmalm's owl. *Oecologia* **126**, 355–359.

HAMEDE, R. K., BASHFORD, J., MCCALLUM, H. & JONES, M. (2009). Contact networks in a wild Tasmanian devil (*Sarcophilus harrisii*) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. *Ecology Letters* **12**, 1147–1157.

HAMILTON, W. D. (1964). The genetical evolution of social behaviour, I and II. *Journal of Theoretical Biology* **7**, 1–52.

*HANSEN, M. J., BUHL, J., BAZAZI, S., SIMPSON, S. J. & SWORD, G. A. (2011). Cannibalism in the lifeboat – collective movement in Australian plague locusts. *Behavioral Ecology and Sociobiology* **65**, 1715–1720.

HANSSON, L.-A. & ÅKESSON, S. (2014). *Animal Movement across Scales*. Oxford University Press, Oxford.

HATCHWELL, B. J. (2009). The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Philosophical Transactions of the Royal Society, B: Biological Sciences* **364**, 3217–3227.

HAWKES, C. (2009). Linking movement behaviour, dispersal and population processes: is individual variation a key? *Journal of Animal Ecology* **78**, 894–906.

HEBBLEWHITE, M. & MERRILL, E. H. (2011). Demographic balancing of migrant and resident elk in a partially migratory population through forage–predation tradeoffs. *Oikos* **120**, 1860–1870.

HEDENSTRÖM, A. (2008). Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philosophical Transactions of the Royal Society, B: Biological Sciences* **363**, 287–299.

HEINSOHN, R., DUNN, P., LEGGE, S. & DOUBLE, M. (2000). Coalitions of relatives and reproductive skew in cooperatively breeding white-winged choughs. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **267**, 243–249.

HENDRY, A. P., BOHLIN, T., JONSSON, B. & BERG, O. K. (2004). To sea or not to sea. In *Evolution Illuminated*, pp. 92–125. Oxford University Press, New York.

HERSKIN, J. & STEFFENSEN, J. F. (1998). Energy savings in sea bass swimming in a school: measurements of tail beat frequency and oxygen consumption at different swimming speeds. *Journal of Fish Biology* **53**, 366–376.

*HIGGINS, K. (2009). Metapopulation extinction risk: dispersal's duplicity. *Theoretical Population Biology* **76**, 146–155.

HINCH, S. G., COOKE, S. J., HEALEY, M. C. & FARRELL, A. P. (2005). Behavioural physiology of fish migrations: salmon as a model approach. *Fish Physiology* **24**, 239–295.

HOLEKAMP, K. E., BOYDSTON, E. E. & SMALE, L. (2000). Group travel in social carnivores. In *On the Move: How and Why Animals Travel in Groups*, pp. 587–627. University of Chicago Press, Chicago.

HORTON, T. W., HOLDAWAY, R. N., ZERBINI, A. N., HAUSER, N., GARRIGUE, C., ANDRIOLO, A. & CLAPHAM, P. J. (2011). Straight as an arrow: humpback whales swim constant course tracks during long-distance migration. *Biology Letters* **7**(5): 674–679 (doi: 10.1098/rsbl.2011.0279).

HOVEL, K. A. & MORGAN, S. G. (1998). Planktivory as a selective force for reproductive synchrony and larval migration. *Oceanographic Literature Review* **3**, 521.

HOVESTADT, T., KUBISCH, A. & POETHKE, H.-J. (2010). Information processing in models for density-dependent emigration: a comparison. *Ecological Modelling* **221**, 405–410.

HUBBARD, S., BABAK, P., SIGURDSSON, S. T. & MAGNÚSSON, K. G. (2004). A model of the formation of fish schools and migrations of fish. *Ecological Modelling* **174**, 359–374.

HUI, A. & PINTER-WOLLMAN, N. (2014). Individual variation in exploratory behaviour improves speed and accuracy of collective nest selection by Argentine ants. *Animal Behaviour* **93**, 261–266.

HUTCHINSON, N., DAVIES, M. S., NG, J. S. S. & WILLIAMS, G. A. (2007). Trail following behaviour in relation to pedal mucus production in the intertidal gastropod *Monodonta labio* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* **349**, 313–322.

IMS, R. A. (1995). Movement patterns related to spatial structures. In *Mosaic Landscapes and Ecological Processes* (eds L. HANSSON, L. FAHRIG and G. MERRIAM), pp. 85–109. Springer Science & Business Media, Belin.

IRISSON, J.-O., PARIS, C. B., LEIS, J. M. & YERMAN, M. N. (2015). With a little help from my friends: group orientation by larvae of a coral reef fish. *PLoS One* **10**, e0144060.

*JACK, K. M. & FEDIGAN, L. (2004). Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 1: patterns and causes of natal emigration. *Animal Behaviour* **67**, 761–769.

JACOB, S., BESTION, E., LEGRAND, D., CLOBERT, J. & COTE, J. (2015*a*). Habitat matching and spatial heterogeneity of phenotypes: implications for metapopulation and metacommunity functioning. *Evolutionary Ecology* **29**, 851–871.

JACOB, S., CHAINE, A. S., SCHTICKZELLE, N., HUET, M. & CLOBERT, J. (2015*b*). Social information from immigrants: multiple immigrant based sources of information for dispersal decisions in a ciliate. *Journal of Animal Ecology* **84**, 1373–1383.

JOHNSTONE, R. A. & MANICA, A. (2011). Evolution of personality differences in leadership. *Proceedings of the National Academy of Sciences* **108**, 8373–8378.

JONZÉN, N., KNUDSEN, E., HOLT, R. D. & SÆTHER, B.-E. (2011). Uncertainty and predictability: the niches of migrants and nomads. In *Animal Migration: A Synthesis*, pp. 91–109. Oxford University Press, Oxford.

*KEISER, C. N., MODLMEIER, A. P., SINGH, N., JONES, D. K. & PRUITT, J. N. (2014). Exploring how a shift in the physical environment shapes individual and group behavior across two social contexts. *Ethology* **120**, 825–833.

KOKKO, H. (2011). Directions in modelling partial migration: how adaptation can cause a population decline and why the rules of territory acquisition matter. *Oikos* **120**, 1826–1837.

KOKKO, H. & LUNDBERG, P. (2001). Dispersal, migration, and offspring retention in saturated habitats. *The American Naturalist* **157**, 188–202.

KOKKO, H. & OTS, I. (2006). When not to avoid inbreeding. *Evolution* **60**, 467–475.

KORPIMÄKI, E., LAGERSTRÖM, M. & SAUROLA, P. (1987). Field evidence for nomadism in Tengmalm's owl *Aegolius funereus*. *Ornis Scandinavica* **18**, 1–4.

KOYKKA, C. & WILD, G. (2015). The evolution of group dispersal with leaders and followers. *Journal of Theoretical Biology* **371**, 117–126.

KRAUSE, J. & RUXTON, G. D. (2002). *Living in Groups*. Oxford University Press, Oxford.

KRUSHELNYCKY, P. D., LOOPE, L. L. & JOE, S. M. (2004). Limiting spread of a unicolonial invasive insect and characterization of seasonal patterns of range expansion. *Biological Invasions* **6**, 47–57.

KÜMMERLI, R., GARDNER, A., WEST, S. A. & GRIFFIN, A. S. (2009). Limited dispersal, budding dispersal, and cooperation: an experimental study. *Evolution* **63**, 939–949.

LAMBIN, X., AARS, J. & PIERTNEY, S. B. (2001). Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the emperical evidence. In *Dispersal* (eds J. CLOBERT, E. DANCHIN, A. A. DHONDT and J. D. NICHOLS), pp. 110–122. Oxford University Press, New York.

Lavelle, M. J., Hygnstrom, S. E., Hildreth, A. M., Campbell, T. A., Long, D. B., Hewitt, D. G., Beringer, J. & VerCauteren, K. C. (2012). Utility of improvised video-camera collars for collecting contact data from white-tailed deer: possibilities in disease transmission studies. *Wildlife Society Bulletin* **36**, 828–834.

*Leca, J. B., Gunst, N., Thierry, B. & Petit, O. (2003). Distributed leadership in semifree-ranging white-faced capuchin monkeys. *Animal Behaviour* **66**, 1045–1052.

*Lee, J.-W., Lee, Y.-K. & Hatchwell, B. J. (2010). Natal dispersal and philopatry in a group-living but noncooperative passerine bird, the vinous-throated parrotbill. *Animal Behaviour* **79**, 1017–1023.

Lefebvre, D., Ménard, N. & Pierre, J. S. (2003). Modelling the influence of demographic parameters on group structure in social species with dispersal asymmetry and group fission. *Behavioral Ecology and Sociobiology* **53**, 402–410.

Le Galliard, J., Ferriere, R. & Clobert, J. (2003). Mother-offspring interactions affect natal dispersal in a lizard. *Proceedings of the Royal Society of London Series B* **270**, 1163–1169.

*Le Goff, G. J., Hance, T., Detrain, C., Deneubourg, J.-L., Clotuche, G. & Mailleux, A.-C. (2012). Impact of starvation on the silk attractiveness in a weaving mite, *Tetranychus urticae* (Acari: Tetranychidae). *Journal of Ethology* **30**, 125–132.

Leis, J. M. (2006). Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology* **51**, 57–141.

Levitan, D. R., Sewell, M. A. & Chia, F.-S. (1992). How distribution and abundance influence fertilization success in the sea urchin *Strongylocentotus franciscanus*. *Ecology* **73**, 248–254.

Liedvogel, M., Åkesson, S. & Bensch, S. (2011). The genetics of migration on the move. *Trends in Ecology & Evolution* **26**, 561–569.

List, C., Elsholtz, C. & Seeley, T. D. (2009). Independence and interdependence in collective decision making: an agent-based model of nest-site choice by honeybee swarms. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 755–762.

Löfgren, O., Hörnfeldt, B. & Carlsson, B.-G. (1986). Site tenacity and nomadism in Tengmalm's owl (*Aegolius funereus* (L.)) in relation to cyclic food production. *Oecologia* **69**, 321–326.

Lohmann, K. J., Putman, N. F. & Lohmann, C. M. F. (2008). Geomagnetic imprinting: a unifying hypothesis of long-distance natal homing in salmon and sea turtles. *Proceedings of the National Academy of Sciences* **105**, 19096–19101.

Loyd, K. A. T., Hernandez, S. M., Carroll, J. P., Abernathy, K. J. & Marshall, G. J. (2013). Quantifying free-roaming domestic cat predation using animal-borne video cameras. *Biological Conservation* **160**, 183–189.

Lucas, M. C., Baras, E., Thom, T. J., Duncan, A. & Slavík, O. (2001). *Migration of Freshwater Fishes*. (Volume 47). Blackwell Science, Oxford.

Lührs, M. & Kappeler, P. (2013). Simultaneous GPS tracking reveals male associations in a solitary carnivore. *Behavioral Ecology and Sociobiology* **67**, 1731–1743.

Lundberg, P. (1988). The evolution of partial migration in birds. *Trends in Ecology & Evolution* **3**, 172–175.

Madsen, J., Cracknell, G. & Fox, T. (1999). *Goose Populations of the Western Palearctic: A Review of Status and Distribution*. National Environmental Research Institute, Rønde.

*Mailleux, A.-C., Fernandez, A. A., San Martin y Gomez, G., Detrain, C. & Deneubourg, J.-L. (2011). Collective migration in house dust mites. *Ethology* **117**, 72–82.

*Maklakov, A. A. (2002). Snake-directed mobbing in a cooperative breeder: anti-predator behaviour or self-advertisement for the formation of dispersal coalitions? *Behavioral Ecology and Sociobiology* **52**, 372–378.

*Mares, R., Bateman, A. W., English, S., Clutton-Brock, T. H. & Young, A. J. (2014). Timing of predispersal prospecting is influenced by environmental, social and state-dependent factors in meerkats. *Animal Behaviour* **88**, 185–193.

Marjamäki, P. H., Contasti, A. L., Coulson, T. N. & McLoughlin, P. D. (2013). Local density and group size interacts with age and sex to determine direction and rate of social dispersal in a polygynous mammal. *Ecology and Evolution* **3**, 3073–3082.

Matthysen, E., Van de Casteele, T. & Adriaensen, F. (2005). Do sibling tits (*Parus major, P. caeruleus*) disperse over similar distances and in similar directions? *Oecologia* **143**, 301–307.

Matthysen, E., Van Overveld, T., Van de Casteele, T. & Adriaensen, F. (2010). Family movements before independence influence natal dispersal in a territorial songbird. *Oecologia* **162**, 591–597.

Mazé-Guilmo, E., Blanchet, S., McCoy, K. D. & Loot, G. (2016). Host dispersal as the driver of parasite genetic structure: a paradigm lost? *Ecology Letters* **19**, 336–347.

McCauley, S. J. & Rowe, L. (2010). *Notonecta* exhibit threat-sensitive, predator-induced dispersal. *Biology Letters* **6**, 449–452.

McClure, M., Ralph, M. & Despland, E. (2011). Group leadership depends on energetic state in a nomadic collective foraging caterpillar. *Behavioral Ecology and Sociobiology* **65**, 1573–1579.

Mercier, A. & Hamel, J.-F. (2010). Synchronized breeding events in sympatric marine invertebrates: role of behavior and fine temporal windows in maintaining reproductive isolation. *Behavioral Ecology and Sociobiology* **64**, 1749–1765.

*Metheny, J. D., Kalcounis-Rueppell, M. C., Bondo, K. J. & Brigham, R. M. (2008). A genetic analysis of group movement in an isolated population of tree-roosting bats. *Proceedings of the Royal Society of London B: Biological Sciences* **275**, 2265–2272.

Milner-Gulland, E., Fryxell, J. M. & Sinclair, A. R. E. (2011). *Animal Migration: A Synthesis*. Oxford University Press, Oxford.

Moll, R. J., Millspaugh, J. J., Beringer, J., Sartwell, J. & He, Z. (2007). A new 'view'of ecology and conservation through animal-borne video systems. *Trends in Ecology & Evolution* **22**, 660–668.

Morgan, S. G. (1990). Impact of planktivorous fishes on dispersal, hatching, and morphology of estuarine crab larvae. *Ecology*, **71**(5), 1640–1652.

Mueller, T. & Fagan, W. F. (2008). Search and navigation in dynamic environments – from individual behaviors to population distributions. *Oikos* **117**, 654–664.

Mueller, T., Olson, K. A., Dressler, G., Leimgruber, P., Fuller, T. K., Nicolson, C., Novaro, A. J., Bolgeri, M. J., Wattles, D., DeStefano, S., Calabrese, J. M. & Fagan, W. F. (2011). How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. *Global Ecology and Biogeography* **20**, 683–694.

Mysterud, A., Loe, L. E., Zimmermann, B., Bischof, R., Veiberg, V. & Meisingset, E. (2011). Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? *Oikos* **120**, 1817–1825.

Nakai, K., Yanagisawa, Y., Sato, T., Niimura, Y. & Gashagaza, M. M. (1990). Lunar synchronization of spawning in cichlid fishes of the tribe Lamprologini in Lake Tanganyika. *Journal of Fish Biology* **37**, 589–598.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* **105**, 19052–19059.

Nathan, R. & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* **15**, 278–285.

Nathan, R., Perry, G., Cronin, J. T., Strand, A. E. & Cain, M. L. (2003). Methods for estimating long-distance dispersal. *Oikos* **103**, 261–273.

Newmaster, S. G., Thompson, I. D., Steeves, R. A., Rodgers, A. R., Fazekas, A. J., Maloles, J. R., McMullin, R. T. & Fryxell, J. M. (2013). Examination of two new technologies to assess the diet of woodland caribou: video recorders attached to collars and DNA barcoding. *Canadian Journal of Forest Research* **43**, 897–900.

*Nichols, H. J., Jordan, N. R., Jamie, G. A., Cant, M. A. & Hoffman, J. I. (2012). Fine-scale spatiotemporal patterns of genetic variation reflect budding dispersal coupled with strong natal philopatry in a cooperatively breeding mammal. *Molecular Ecology* **21**, 5348–5362.

Noordwijk, A., Pulido, F., Helm, B., Coppack, T., Delingat, J., Dingle, H., Hedenström, A., Jeugd, H., Marchetti, C., Nilsson, A. & Pérez-Tris, J. (2006). A framework for the study of genetic variation in migratory behaviour. *Journal of Ornithology* **147**, 221–233.

Northcote, T. G. (1978). Migratory strategies and production of freshwater fishes. In *Ecology of Freshwater Fish Production* (eds S. D. Gerking, p. 326–359. Ecology of Freshwater Fish Production, Blackwell Science, Oxford.

Olsson, I. C., Greenberg, L. A., Bergman, E. & Wysujack, K. (2006). Environmentally induced migration: the importance of food. *Ecology Letters* **9**, 645–651.

Páez, D. J., Brisson-Bonenfant, C., Rossignol, O., Guderley, H. E., Bernatchez, L. & Dodson, J. J. (2011). Alternative developmental pathways and the propensity to migrate: a case study in the Atlantic salmon. *Journal of Evolutionary Biology* **24**, 245–255.

Pasinelli, G., Schiegg, K. & Walters, J. R. (2004). Genetic and environmental influences on natal dispersal distance in a resident bird species. *The American Naturalist* **164**, 660–669.

Pedler, R. D., Ribot, R. F. H. & Bennett, A. T. D. (2014). Extreme nomadism in desert waterbirds: flights of the banded stilt. *Biology Letters* **10**, 20140547.

Penkov, S., Ogawa, A., Schmidt, U., Tate, D., Zagoriy, V., Boland, S., Gruner, M., Vorkel, D., Verbavatz, J.-M., Sommer, R. J., Knölker, H.-J. & Kurzchalia, T. V. (2014). A wax ester promotes collective host finding in the nematode *Pristionchus pacificus*. *Nature Chemical Biology* **10**, 281–285.

Pennekamp, F., Mitchell, K. A., Chaine, A. & Schtickzelle, N. (2014). Dispersal propensity in *Tetrahymena thermophila* ciliates—a reaction norm perspective. *Evolution* **68**, 2319–2330.

Perrin, N. & Mazalov, V. (2000). Local competition, inbreeding, and the evolution of sex-biased dispersal. *The American Naturalist* **155**, 116–127.

Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V. & Bennett, V. J. (2005). Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. *Ecology* **86**, 2386–2396.

Poethke, H. J., Gros, A. & Hovestadt, T. (2011). The ability of individuals to assess population density influences the evolution of emigration propensity and dispersal distance. *Journal of Theoretical Biology* **282**, 93–99.

*Pope, T. R. (2000). Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). *Behavioral Ecology and Sociobiology* **48**, 253–267.

Prange, S., Jordan, T., Hunter, C. & Gehrt, S. D. (2006). New radiocollars for the detection of proximity among individuals. *Wildlife Society Bulletin* **34**, 1333–1344.

Pringle, J. M., Byers, J. E., Pappalardo, P., Wares, J. P. & Marshall, D. (2014). Circulation constrains the evolution of larval development modes and life histories in the coastal ocean. *Ecology* **95**, 1022–1032.

Pulido, F. (2007). The genetics and evolution of avian migration. *Bioscience* **57**, 165–174.

Pulido, F. & Berthold, P. (2010). Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. *Proceedings of the National Academy of Sciences* **107**, 7341–7346.

Pulido, F., Berthold, P., Mohr, G. & Querner, U. (2001). Heritability of the timing of autumn migration in a natural bird population. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **268**, 953–959.

Quinn, T. P. (1993). Biological interactions of natural and enhanced stocks of salmon. A review of homing and straying of wild and hatchery-produced salmon. *Fisheries Research* **18**, 29–44.

Ramenofsky, M. & Wingfield, J. C. (2007). Regulation of migration. *Bioscience* **57**, 135–143.

*Randall, J. A., Rogovin, K., Parker, P. G. & Eimes, J. A. (2005). Flexible social structure of a desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints. *Behavioral Ecology* **16**, 961–973.

Rangel, J., Griffin, S. R. & Seeley, T. D. (2010). An oligarchy of nest-site scouts triggers a honeybee swarm's departure from the hive. *Behavioral Ecology and Sociobiology* **64**, 979–987.

Ridley, A. (2012). Invading together: the benefits of coalition dispersal in a cooperative bird. *Behavioral Ecology and Sociobiology* **66**, 77–83.

*Rittschof, C. C. & Seeley, T. D. (2008). The buzz-run: how honeybees signal 'Time to go!'. *Animal Behaviour* **75**, 189–197.

Rodway, M. S. (2007). Timing of pairing in waterfowl I: reviewing the data and extending the theory. *Waterbirds* **30**, 488–505.

Rogers, A. R. (1987). A model of kin-structured migration. *Evolution* **41**(2), 417–426.

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.

Ronce, O. & Clobert, J. (2012). Dispersal syndromes. In *Dispersal. Ecology and Evolution* (eds J. Clobert, M. Baguette, T. G. Benton, J. M. Bullock and S. Ducatez). p. 119–138. Oxford University Press, New York.

Roshier, D. & Reid, J. (2003). On animal distributions in dynamic landscapes. *Ecography* **26**, 539–544.

Rutz, C., Bluff, L. A., Weir, A. A. & Kacelnik, A. (2007). Video cameras on wild birds. *Science* **318**, 765.

Rutz, C. & Troscianko, J. (2013). Programmable, miniature video-loggers for deployment on wild birds and other wildlife. *Methods in Ecology and Evolution* **4**, 114–122.

Sala, E., Ballesteros, E. & Starr, R. M. (2001). Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. *Fisheries* **26**, 23–30.

Salewski, V. & Bruderer, B. (2007). The evolution of bird migration—a synthesis. *Naturwissenschaften* **94**, 268–279.

Schauber, E. M., Storm, D. J. & Nielsen, C. K. (2007). Effects of joint space use and group membership on contact rates among white-tailed deer. *The Journal of Wildlife Management* **71**, 155–163.

Schjorring, S. (2002). The evolution of informed natal dispersal: inherent versus acquired information. *Evolutionary Ecology Research* **4**, 227–238.

Schmaljohann, H. & Naef-Daenzer, B. (2011). Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird. *Journal of Animal Ecology* **80**, 1115–1122.

*Schoof, V., Jack, K. & Isbell, L. (2009). What traits promote male parallel dispersal in primates? *Behaviour* **146**, 701–726.

Schtickzelle, N., Fjerdingstad, E., Chaine, A. & Clobert, J. (2009). Cooperative social clusters are not destroyed by dispersal in a ciliate. *BMC Evolutionary Biology* **9**, 251.

*Schũlke, O., Bhagavatula, J., Vigilant, L. & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology* **20**, 2207–2210.

Schwarzkopf, L. & Alford, R. A. (2002). Nomadic movement in tropical toads. *Oikos* **96**, 492–506.

Selkoe, K. A., Gaines, S. D., Caselle, J. E. & Warner, R. R. (2006). Current shifts and kin aggregation explain genetic patchiness in fish recruits. *Ecology* **87**, 3082–3094.

Shapiro, D. Y. (1983). On the possibility of kin groups in coral reef fishes. In *Ecology of Deep and Shallow Reefs* (eds M.L. Reaka, pp. 39–45. The ecology of deep and shallow coral reefs. Symposia Series for Undersea Research, NOAA's Undersea Research Program. U.S. Department of Commerce Vol. 1 No. 1.

Sharp, S. P., Simeoni, M. & Hatchwell, B. J. (2008). Dispersal of sibling coalitions promotes helping among immigrants in a cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences* **275**, 2125–2130.

Shaw, A. K. & Couzin, I. D. (2013). Migration or residency? The evolution of movement behavior and information usage in seasonal environments. *The American Naturalist* **181**, 114–124.

Shima, J. S. & Swearer, S. E. (2016). Evidence and population consequences of shared larval dispersal histories in a marine fish. *Ecology* **97**, 25–31.

Siegel, D. A., Mitarai, S., Costello, C. J., Gaines, S. D., Kendall, B. E., Warner, R. R. & Winters, K. B. (2008). The stochastic nature of larval connectivity among nearshore marine populations. *Proceedings of the National Academy of Sciences* **105**, 8974–8979.

Simons, A. M. (2004). Many wrongs: the advantage of group navigation. *Trends in Ecology & Evolution* **19**, 453–455.

*Simpson, S. J., Sword, G. A., Lorch, P. D. & Couzin, I. D. (2006). Cannibal crickets on a forced march for protein and salt. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 4152–4156.

Sinervo, B., Calsbeek, R., Comendant, T., Both, C., Adamopoulou, C. & Clobert, J. (2006). Genetic and maternal determinants of effective dispersal: the effect of sire genotype and size at birth in side-blotched lizards. *The American Naturalist* **168**, 88–99.

Snyder, R. J. (1991). Migration and life histories of the threespine stickleback: evidence for adaptive variation in growth rate between populations. *Environmental Biology of Fishes* **31**, 381–388.

Stamps, J. A. (2001). Habitat selection by dispersers: integrating proximate and ultimate approaches. In *Dispersal* (eds J. Clobert, E. Danchin, A. A. Dhondt and J. D. Nichols), pp. 110–122. Oxford University Press, New York.

*Steckenreuter, A., Harcourt, R. & Moeller, L. (2011). Distance does matter: close approaches by boats impede feeding and resting behaviour of Indo-Pacific bottlenose dolphins. *Wildlife Research* **38**, 455–463.

Stevens, V. M., Whitmee, S., Le Galliard, J.-F., Clobert, J., Böhning-Gaese, K., Bonte, D., Brändle, M., Matthias Dehling, D., Hof, C., Trochet, A. & Baguette, M. (2014). A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. *Ecology Letters* **17**, 1039–1052.

*Stoinski, T. S., Vecellio, V., Ngaboyamahina, T., Ndagijimana, F., Rosenbaum, S. & Fawcett, K. A. (2009). Proximate factors influencing dispersal decisions in male mountain gorillas, *Gorilla beringei beringei*. *Animal Behaviour* **77**, 1155–1164.

Strathmann, R. R., Hughes, T. P., Kuris, A. M., Lindeman, K. C., Morgan, S. G., Pandolfi, J. M. & Warner, R. R. (2002). Evolution of local recruitment and its consequences for marine populations. *Bulletin of Marine Science* **70**, 377–396.

Sumpter, D. J. T. (2010). *Collective Animal Behavior*. Princeton University Press, Princeton.

Sumpter, D. J. T. & Pratt, S. C. (2009). Quorum responses and consensus decision making. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **364**, 743–753.

Szulkin, M. & Sheldon, B. C. (2008). Dispersal as a means of inbreeding avoidance in a wild bird population. *Proceedings of the Royal Society B: Biological Sciences* **275**, 703–711.

Szulkin, M., Stopher, K. V., Pemberton, J. M. & Reid, J. M. (2013). Inbreeding avoidance, tolerance, or preference in animals? *Trends in Ecology & Evolution* **28**, 205–211.

Tambling, C. J. & Belton, L. E. (2009). Feasibility of using proximity tags to locate female lion Panthera leo kills. *Wildlife Biology* **15**, 435–441.

Toonen, R. J. & Pawlik, J. R. (2001). Foundations of gregariousness: a dispersal polymorphism among the planktonic larvae of a marine invertebrate. *Evolution* **55**, 2439–2454.

Torney, C., Neufeld, Z. & Couzin, I. D. (2009). Context-dependent interaction leads to emergent search behavior in social aggregates. *Proceedings of the National Academy of Sciences* **106**, 22055–22060.

Travis, J. M. J., Murrell, D. J. & Dytham, C. (1999). The evolution of density-dependent dispersal. *Proceedings: Biological Sciences* **266**, 1837–1842.

Travis, J. M. J., Mustin, K., Barton, K. A., Benton, T. G., Clobert, J., Delgado, M. M., Dytham, C., Hovestadt, T., Palmer, S. C. F., Van Dyck, H. & Bonte, D. (2012). Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. *Methods in Ecology and Evolution* **3**, 628–641.

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.

Tschirren, B., Fitze, P. S. & Richner, H. (2007). Maternal modulation of natal dispersal in a passerine bird: an adaptive strategy to cope with parasitism? *The American Naturalist* **169**, 87–93.

Valone, T. J. (1989). Group foraging, public information, and patch estimation. *Oikos* **56**, 357–363.

Valsecchi, E., Hale, P., Corkeron, P. & Amos, W. (2002). Social structure in migrating humpback whales (*Megaptera novaeangliae*). *Molecular Ecology* **11**, 507–518.

Vardanis, Y., Klaassen, R. H. G., Strandberg, R. & Alerstam, T. (2011). Individuality in bird migration: routes and timing. *Biology Letters* **7**, 502–505.

Végvári, Z., Barta, Z., Mustakallio, P. & Székely, T. (2011). Consistent avoidance of human disturbance over large geographical distances by a migratory bird. *Biology Letters* **7**, 814–817.

*Wang, C. & Lu, X. (2014). Dispersal in kin coalition throughout the non-breeding season to facilitate fine-scale genetic structure in the breeding season: evidence from a small passerine. *Ethology* **120**, 1003–1012.

Weimerskirch, H., Martin, J., Clerquin, Y., Alexandre, P. & Jiraskova, S. (2001). Energy saving in flight formation. *Nature* **413**, 697–698.

West, S. A., Pen, I. & Griffin, A. S. (2002). Cooperation and competition between relatives. *Science* **296**, 72–75.

Wey, T. W., Spiegel, O., Montiglio, P.-O. & Mabry, K. E. (2015). Natal dispersal in a social landscape: considering individual behavioral phenotypes and social environment in dispersal ecology. *Current Zoology* **61**, 543–556.

van Wijk, R. E., Kölzsch, A., Kruckenberg, H., Ebbinge, B. S., Müskens, G. J. D. M. & Nolet, B. A. (2012). Individually tracked geese follow peaks of temperature acceleration during spring migration. *Oikos* **121**, 655–664.

Wikberg, E. C., Jack, K. M., Campos, F. A., Fedigan, L. M., Sato, A., Bergstrom, M. L., Hiwatashi, T. & Kawamura, S. (2014). The effect of male parallel dispersal on the kin composition of groups in white-faced capuchins. *Animal Behaviour* **96**, 9–17.

Williams, D. A. & Rabenold, K. N. (2005). Male-biased dispersal, female philopatry, and routes to fitness in a social corvid. *Journal of Animal Ecology* **74**, 150–159.

Winkler, D. W., Greenberg, R. & Marra, P. (2005). How do migration and dispersal interact. In *Birds of Two Worlds: The Ecology and Evolution of Migration*, pp. 401–413. The Johns Hopkins University Press, Baltimore.

Wooster, D. & Sih, A. (1995). A review of the drift and activity responses of stream prey to predator presence. *Oikos* **73**, 3–8.

Yano, S. (2008). Collective and solitary behaviors of twospotted spider mite (Acari: Tetranychidae) are induced by trail following. *Annals of the Entomological Society of America* **101**, 247–252.

*Yao, H., Liu, X., Stanford, C., Yang, J., Huang, T., Wu, F. & Li, Y. (2011). Male dispersal in a provisioned multilevel group of *Rhinopithecus roxellana* in Shennongjia Nature Reserve, China. *American Journal of Primatology* **73**, 1280–1288.

Yearsley, J. M., Viard, F. & Broquet, T. (2013). The effect of collective dispersal on the genetic structure of a subdivided population. *Evolution* **67**, 1649–1659.

Yoder, J. M., Marschall, E. A. & Swanson, D. A. (2004). The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology* **15**, 469–476.

Zera, A. J. & Brisson, J. A. (2012). Quantitative, physiological, and molecular genetics of dispersal and migration. In *Dispersal. Ecology and Evolution* (eds J. Clobert, M. Baguette, T. G. Benton, J. M. Bullock and S. Ducatez), p. 63–82. Oxford University Press, New York.

*Zirbes, L., Deneubourg, J.-L., Brostaux, Y. & Haubruge, E. (2010). A new case of consensual decision: collective movement in earthworms. *Ethology* **116**, 546–553.

IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Data from published literature on collective dispersal.

(*Received 18 December 2015; revised 23 March 2016; accepted 6 April 2016; published online 6 May 2016*)