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

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3 **1 Behavioral synchronization of large-scale animal movements – disperse**
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5 **2 alone, but migrate together?**
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31 **ABSTRACT**

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

49
50 Keywords: dispersal, seasonal migration, social grouping, coalition, budding, transience,
51 sociability, parallel dispersal, schooling, coordinated movement

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74 I. INTRODUCTION

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

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3 82 There is a broad consensus on the main functions of movement: organisms may move
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5 83 i/ to satisfy their basic immediate requirements such as food, shelter or mates (“foraging”
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7 84 *movements*), ii/ to relocate their home range to a novel area in response to social or
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9 85 environmental stimuli (*dispersal*), which potentially leads to gene flow, or iii/ to escape
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11 86 temporarily adverse environmental conditions through periodic out and back movements
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13 87 (*migration*). Several attempts have been made to translate this teleological view into more or
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15 88 less exclusive categories in relation to the *spatio-temporal scale* and the *behavior* of the
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17 89 organism, moving within or outside of their usual home range (Ims, 1995; Dingle & Drake,
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19 90 2007; Dingle, 2014).

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24 91 Considering the *spatio-temporal scale*, foraging involves frequent, short-distance
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26 92 (within-patch) movements to locate resources; dispersal occurs at a larger spatial scale and is
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28 93 limited in time to movements from the natal site to the first breeding site (i.e. natal dispersal),
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30 94 or between successive breeding locations (i.e. breeding dispersal); migration is the recurrent,
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32 95 two-way out and back movement of individuals between spatially distinct areas which
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34 96 provide favorable ecological conditions for given periods of time or seasons (Nathan *et al.*,
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36 97 2008; Hansson & Åkesson, 2014).

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40 98 Considering *behavior*, foraging individuals interrupt their movement within their
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42 99 home range when a suitable **food** resource is encountered. This also holds true for dispersing
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44 100 individuals, with the difference that dispersing individuals move outside of their current home
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46 101 range **to locate a new breeding site**. Migrating individuals also move outside of their home
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48 102 range, but their displacements are not necessarily interrupted when they encounter a suitable
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50 103 resource (Dingle & Drake, 2007; Dingle, 2014). Note that these two viewpoints of
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52 104 movement categories are not exclusive (see Section IV for further discussion).
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3 105 These three main types of movements (foraging, dispersal and migration) are clearly
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5 106 not independent: they all rely on the same locomotory system and, to a lesser extent, on the
6
7 107 same orientation, navigation and memory mechanisms (Nathan *et al.*, 2008; Burgess *et al.*,
8
9 108 2015). However, depending on the organism's life history, one type of movement may be
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11 109 under stronger selective pressures than the others. This may lead to particular morphological
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13 110 and/or physiological specializations of the locomotory and associated systems which may, in
14
15 111 turn, constrain the other types of movement (Hansson & Åkesson, 2014).

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18 112 Although social context is often assumed to be an important external driver of
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20 113 movements, inter-individual dependency during large-scale movement remains poorly
21
22 114 understood (Mueller & Fagan, 2008; Nathan *et al.*, 2008; Travis *et al.*, 2012; Bauer &
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24 115 Klaassen, 2013). Dispersal is generally seen as a solitary enterprise so that the influence of
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26 116 the dispersal behavior of conspecifics on an individual's dispersal decisions and, in particular,
27
28 117 the potential for inter-individual synchronization during dispersal movements, is rarely
29
30 118 considered. For example, in western mosquitofish (*Gambusia affinis*), individual and
31
32 119 population levels of asocial behavior negatively correlate with schooling behavior (Cote,
33
34 120 Fogarty, & Sih, 2012) and positively influence dispersal propensity and distance (Cote *et al.*,
35
36 121 2011). Indeed, when reviewing the dispersal literature for evidence of collective movements,
37
38 122 we found only forty-two empirical studies (out of 788 papers between 2000 and 2015) that
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40 123 mentioned keys related to collective dispersal, while six theoretical studies modeled this
41
42 124 process (See Appendix S1 in Supporting Information). This is in stark contrast with the recent
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44 125 focus on socially informed dispersal (Clobert *et al.*, 2009), where decisions about departure
45
46 126 and settlement are based on social cues such as the performance and dispersal behavior of
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48 127 others (Doligez, Danchin, & Clobert, 2002; Doligez *et al.*, 2003; Cote & Clobert, 2007a,
49
50 128 2010; Boulinier *et al.*, 2008; De Meester & Bonte, 2010; Fronhofer, Kropf, & Altermatt,
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52 129 2015b; Jacob *et al.*, 2015b). The widespread occurrence of informed dispersal (Clobert *et al.*,
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3 130 2009) highlights the need to understand inter-individual synchronization in movements during
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5 131 the dispersal process. Comparison with other large-scale movements, specifically seasonal
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7 132 migration, might be a fruitful way of doing so. Indeed, although dispersal and migration are
8
9 133 two superficially similar large-scale movements, they appear to differ in terms of the
10
11 134 importance of inter-individual behavioral synchronization. While for many people the word
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13 135 migration commonly conjures up images of enormous caribou herds traipsing a thousand
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15 136 kilometers across the arctic tundra, or massive groups of wildebeest searching for water and
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17 137 seasonal grazing in the East African savannah, animals of almost all species are generally
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19 138 thought to disperse alone. By comparing proximate and ultimate factors driving dispersal and
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21 139 migration, we may better understand when and why we should expect inter-individual
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23 140 behavioral synchronization of one or both types of movement (Fig. 1).
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28 141 Both dispersal and migration involve three steps: individuals leave their current habitat
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30 142 patch (here defined as an area of sufficient size and resources for an individual to be able to
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32 143 maintain itself for a given period of time; natal or breeding range for dispersal; breeding or
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34 144 wintering range for migration), travel across the landscape (i.e. transience), and finally settle
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36 145 in a novel habitat patch (i.e. settlement; breeding range for dispersal; breeding or wintering
37
38 146 range for migration). For both dispersal and migration, inter-individual synchronization, either
39
40 147 temporal and/or spatial, may be a specific feature of each of these three movement steps.
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42 148 Certain individuals of a given population may leave their respective habitat patches at the
43
44 149 same time (i.e. temporal synchronization). Subsequently, during transience, individuals may
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46 150 travel together (i.e. temporal and spatial synchronization), or use the same path at different
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48 151 times (i.e. spatial synchronization). Finally, individuals may arrive at their destination at the
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50 152 same time (i.e. temporal synchronization) and/or settle in the same habitat patch (i.e. spatial
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52 153 synchronization). Across these three steps, almost all combinations of temporal and spatial
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54 154 synchronization are possible. For example, individuals may leave at the same time, but move
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1
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3 155 towards different locations, or leave at different times, but take the same path across the
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5 156 landscape. Here, we discuss the behavioral components of temporal and spatial
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7 157 synchronization at each step for dispersal and seasonal migration, and we explore how any
8
9 158 differences may be linked to the ultimate factors driving dispersal and migration. We
10
11 159 subsequently focus on dispersal, highlighting how, until now, synchronization in movement
12
13 160 has largely been ignored in dispersal theory. We emphasize why it is important to consider
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15 161 behavioral synchronization during dispersal, both in terms of our fundamental understanding
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17 162 of ecological and evolutionary processes, as well as for improving predictions of species'
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19 163 responses to current environmental change. Finally, we establish how a synthesis among the
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21 164 fields of dispersal, migration and collective movements may advance our understanding of the
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23 165 social context of inter-individual synchronization in dispersal behaviors, both in terms of
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25 166 developing new theory and collecting empirical data. We thereby identify a new, largely
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27 167 unexplored and potentially crucially important field for future research.
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33 **II. DISPERSAL**

34 **(1) Synchronization of departure**

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37 170 By dispersing, individuals are able to escape from their abiotic and biotic environment.
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39 171 Specifically, individuals may disperse away from their natal or breeding habitat patch *i/* to
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41 172 avoid competition with kin and/or non-kin conspecifics and with heterospecifics (Byers,
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43 173 2000; Lambin, Aars, & Piernney, 2001; Le Galliard, Ferriere, & Clobert, 2003; Bitume *et al.*,
44
45 174 2013; Fronhofer *et al.*, 2015a, 2015b), *ii/* to avoid mating with related individuals and, hence,
46
47 175 inbreeding (Perrin & Mazalov, 2000; Szulkin & Sheldon, 2008) or *iii/* in response to adverse
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49 176 abiotic and/or biotic conditions (e.g. low resource availability: Byers, 2000; adverse climatic
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51 177 conditions: Bonte *et al.*, 2008; Bestion, Clobert, & Cote, 2015; predation risk: Wooster &
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53 178 Sih, 1995; Gilliam & Fraser, 2001; Hakkarainen *et al.*, 2001; McCauley & Rowe, 2010;
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55 179 Bestion *et al.*, 2014). This complex causality generates substantial variation among
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3 180 individuals in dispersal behavior, for example, in the timing of dispersal. First, different
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5 181 ecological factors may induce individual dispersal at different life stages. For example, high
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7 182 levels of kin competition and/or inbreeding are likely to influence the natal dispersal decision,
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9 183 i.e. prior to reproduction (Cote, Clobert, & Fitze, 2007; Szulkin & Sheldon, 2008; Bitume *et*
10
11 184 *al.*, 2013), while variation in population density and/or predation risk may induce dispersal at
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13 185 any life stage, or even affect the dispersal decision in contrasting ways at different life stages
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15 186 (e.g. Le Galliard *et al.*, 2003; Marjamäki *et al.*, 2013). Second, within a given life stage,
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17 187 individuals may experience contrasting local conditions because of spatial and temporal
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19 188 heterogeneity. For example, predators and conspecifics are usually heterogeneously
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21 189 distributed across a given habitat patch (Fryxell *et al.*, 2007). The time needed to assess
22
23 190 levels of competition and predation risk will thus vary among individuals. As a consequence,
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25 191 even if individuals ultimately take the same dispersal decision, environmental heterogeneity
26
27 192 makes temporal synchronization of departure less likely. Third, dispersal decisions are most
28
29 193 often phenotype- and context-dependent, driven by the complex interaction between an
30
31 194 individual's phenotype and the prevailing ecological context (Bowler & Benton, 2005;
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33 195 Clobert *et al.*, 2009; Cote *et al.*, 2010; Burgess *et al.*, 2015; Wey *et al.*, 2015; Jacob *et al.*,
34
35 196 2015a), including competition, predation risk and abiotic conditions (Byers, 2000; Gilliam &
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37 197 Fraser, 2001; Cote & Clobert, 2007b; Bonte *et al.*, 2008; Cote *et al.*, 2013; Pennekamp *et*
38
39 198 *al.*, 2014; Bestion *et al.*, 2015). For example, more active individuals experience higher
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41 199 predation risk (e.g. Yoder, Marschall, & Swanson, 2004), while larger individuals are
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43 200 generally better competitors (Garant *et al.*, 2005). The interaction between abiotic and/or
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45 201 biotic conditions and inter-individual phenotypic heterogeneities should thus create
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47 202 asynchrony in the timing of dispersal among individuals, even if they disperse for the same
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49 203 ultimate reason. Overall, the above factors might explain why dispersal is often perceived to
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51 204 be an individual decision rather than a collective one.
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3 205 However, synchronized dispersal departure has occasionally been observed. The 42
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5 206 empirical studies from our literature search covered a limited range of taxonomic groups (30
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7 207 taxa, 1 on nematodes, 15 studies on arthropods, 2 on fish, 7 on birds, and 12 on mammals),
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9 208 with some dominant taxonomic groups (12 studies on primates). Although these studies
10
11 209 mostly involved eusocial species, species with some cooperative behaviors, or species living
12
13 210 in groups without overt cooperation (N = 35 out of 42 studies), seven studies reported that
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15 211 solitary/non-eusocial species formed groups for at least one dispersal stage. In non-eusocial
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17 212 species, individuals may leave their habitat patch simultaneously and travel in a coordinated
18
19 213 manner when local conditions at that given moment in time affect a number of individuals
20
21 214 similarly. For example, Burghardt, Greene, & Rand (1977) showed that green iguana
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23 215 hatchlings (*Iguana iguana*) often leave their natal patch in groups of 2 to 10 individuals,
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25 216 moving together in the same direction, because this decreases predation risk. Similarly, in the
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27 217 two-spotted spider mite (*Tetranychus urticae*), a sub-social species, individuals may disperse
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29 218 alone (i.e. walking or ballooning), or collectively (i.e. as a silk ball) under conditions of
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31 219 overcrowding or food shortage (Yano, 2008; Clotuche *et al.*, 2011). Intuitively, individuals
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33 220 that are born within a narrow time window are more likely to experience similar local
34
35 221 conditions and so to display temporal synchronization in natal dispersal. This has been well-
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37 222 illustrated in marine species (Burgess *et al.*, 2015) where, although dispersal is assumed to be
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39 223 a stochastic process in species with larval forms, it may actually occur in a highly
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41 224 synchronized manner (Leis, 2006; Siegel *et al.*, 2008; Bernardi *et al.*, 2012; Ben-Tzvi *et al.*,
42
43 225 2012; Broquet, Viard, & Yearsley, 2013; Burgess *et al.*, 2015; Irisson *et al.*, 2015). Indeed,
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45 226 in these species, the dispersal phases depend on the timing and location of spawning, on
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47 227 vertical migration in the water column, on pelagic larval development and on ocean currents
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49 228 (e.g. Bonhomme & Planes, 2000; Strathmann *et al.*, 2002; Pringle *et al.*, 2014; Burgess *et*
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51 229 *al.*, 2015). A single individual, and even multiple individuals, often release all their gametes
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3 230 or larvae into the water at the same time (Shapiro, 1983; Alino & Coll, 1989; Mercier &
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5 231 Hamel, 2010). For broadcast spawners, releasing sperm and egg, synchronized releases may
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7 232 increase the aggregation of gametes and therefore the success of fertilization (Levitan, Sewell,
8
9 233 & Chia, 1992) or may be triggered by environmental factors (Alino & Coll, 1989; Mercier &
10
11 234 Hamel, 2010). The release of eggs or larvae may also be synchronized in brooders because of
12
13 235 external conditions that may synchronize spawning or may enhance progeny survival
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15 236 prospects, e.g. using the ebbing tide to flush eggs and larvae away from benthic predators or
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17 237 nearshore environments not conducive to pelagic larval development (Alino & Coll, 1989;
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19 238 Nakai *et al.*, 1990; Mercier & Hamel, 2010). These synchronized releases could result in
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21 239 passively synchronized dispersal departure. In addition, candidate dispersers may actively
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23 240 postpone their departure until environmental conditions are optimal in order to increase their
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25 241 dispersal success which should also favor temporal synchronization in departure.
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29 242 **Actively synchronized** departure appears to be more common among both
30
31 243 invertebrates and vertebrates of eusocial and cooperative species. An extreme example is
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33 244 group fission, where an increase in group size or severe external conditions leads to the
34
35 245 splitting of a single group or entity into two or more groups, often, but not always, based on
36
37 246 relatedness (Lefebvre, Ménard, & Pierre, 2003; Rangel, Griffin, & Seeley, 2010). For
38
39 247 example, in social insects, colonies reproduce by fission where a part of the population (e.g.
40
41 248 old queen and workers) flies together in a swarm to locate a new nest site, with take-off being
42
43 249 induced by signals from nest-site scouts (Rangel *et al.*, 2010).
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47 250 A somewhat less striking example concerns coalitions in cooperative species. In many
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49 251 cooperative breeders, offspring delay dispersal and become helpers (Cockburn, 1998;
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51 252 Hatchwell, 2009). Subsequently, some individuals may disperse alone or in small coalitions
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53 253 to become helpers or breeders in neighboring groups (Bergmüller *et al.*, 2005; Wikberg *et al.*,
54
55 254 2014). Dispersal coalitions are also often made up of related individuals (Sharp, Simeoni, &
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3 255 Hatchwell, 2008; Wikberg *et al.*, 2014). For example, Sharp *et al.* (2008) observed kin
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5 256 coalitions and kin-biased helping in dispersing long-tailed tits (*Aegithalos caudatus*).
6
7 257 Similarly, in cooperatively breeding brown jays (*Cyanocorax morio*), related males formed
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9 258 coalitions and dispersed to groups with other male relatives (Williams & Rabenold, 2005).
10
11 259 These kin coalitions increase the probability of gaining access to reproduction and reduce the
12
13 260 costs of integrating into another group (Heinsohn *et al.*, 2000; Williams & Rabenold, 2005;
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15 261 Sharp *et al.*, 2008; Ridley, 2012; van Dongen *et al.*, 2014, reviewed in Hatchwell, 2009).
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20 262 At a proximate level, siblings generally share a common pre-dispersal environment,
21
22 263 including the maternal environment and the levels of inbreeding and kin competition, and
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24 264 often display phenotypic similarities (i.e. family effects, *sensu* Gaillard *et al.*, 1998). In
25
26 265 addition, siblings are born in the same location and share the same potential dispersal
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28 266 destinations. We would thus expect siblings to take similar dispersal decisions with similar
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30 267 timing; however, there is virtually no empirical information on the dispersal behaviour of
31
32 268 siblings in wild populations. Some preliminary data from a detailed long-term study of roe
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34 269 deer (see Debeffe *et al.*, 2012 for details) on the dispersal fates of twin litter-mates monitored
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36 270 by GPS telemetry indicated some degree of synchronisation in dispersal behaviour within
37
38 271 litters, but this synchronisation was never both spatial and temporal together. While litter
39
40 272 mates generally made the same dispersal decision, either to disperse or to remain philopatric,
41
42 273 and left the natal range at approximately the same time (i.e. during the same week), in most
43
44 274 cases synchronization during transience and settlement was low or absent. Hence, natal
45
46 275 dispersal of roe deer seems to be essentially an asocial behavior, even among litter mates,
47
48 276 which contrasts with the highly synchronized migration behavior observed in certain
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50 277 populations of the same species (Danilkin & Hewison, 1996). This lack of synchronization in
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52 278 the settlement behavior of dispersing siblings is coherent with the hypothesis that natal and
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3 279 breeding dispersal are largely driven by selection for inbreeding avoidance in this generally
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5 280 highly sedentary species (Debeffe *et al.*, 2014).
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8
9 281 The dispersal of kin coalitions, also called budding dispersal, has some theoretical
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11 282 support and has been hypothesized to promote the evolution of cooperation. Limited dispersal
12
13 283 is believed to favor the evolution of cooperation (Hamilton, 1964; Schtickzelle *et al.*, 2009)
14
15 284 but, at the same time, to increase competition among relatives (West, Pen, & Griffin, 2002).
16
17 285 This means that dispersal should have little or no influence on the evolution of cooperation.
18
19 286 Budding dispersal, where related individuals disperse in groups, may favor cooperation
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21 287 because it decreases kin competition while maintaining high levels of relatedness
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23 288 (Krushelnycky, Loope, & Joe, 2004; Gardner & West, 2006; Kümmerli *et al.*, 2009; Hui &
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25 289 Pinter-Wollman, 2014; Koykka & Wild, 2015).
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30 31 291 **(2) Temporal synchronization in transience and settlement**

32
33 292 The temporal synchronization of departure, transience and settlement should be
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35 293 strongly interconnected. Temporal synchronization of transience and settlement probably only
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37 294 occurs when departure is also synchronized in time, whereas synchronized departure does not
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39 295 always lead to synchronized transience. Budding dispersal in cooperative species almost
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41 296 always involves leaving, travelling and settling together (Cockburn, 1998; Hatchwell, 2009),
42
43 297 while dispersal in response to common local conditions is more likely to lead to synchronized
44
45 298 departure only. However, synchronized transience may also result from similarities in
46
47 299 environmental drivers of dispersal. For example, synchronized spawning in aquatic species
48
49 300 may lead to similarities in the direction or the distance moved when the dispersal path is
50
51 301 driven by environmental factors as in passive dispersers (e.g. ocean currents, Pringle *et al.*,
52
53 302 2014) or when active dispersers coordinate their behavior during transience (Leis, 2006;
54
55 303 Irisson *et al.*, 2015). There is some indirect evidence that larvae may disperse together
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3 304 (Bernardi *et al.*, 2012; Ben-Tzvi *et al.*, 2012; Shima & Swearer, 2016). For instance, using
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5 305 otolith micro-chemistry, Ben-Tzvi *et al.* (2012) showed that larvae of the coral-reef
6
7 306 damselfish *Neopomacentrus miryae* likely remain in cohesive cohorts of unrelated individuals
8
9
10 307 during the 28 days of dispersal, from hatching to settlement.

11
12 Travelling and settling in groups is associated with benefits (e.g. decreased predation
13
14 309 risk, higher integration success) and costs (e.g. consensus costs) which are similar in nature to
15
16 310 those of group living (Krause & Ruxton, 2002; Conradt & Roper, 2005; Couzin *et al.*,
17
18 311 2005). Animals travelling in groups may benefit both directly and indirectly from the
19
20 312 presence of other group members. More experienced individuals may, for example, improve
21
22 313 group navigation (Simons, 2004). Some individuals from a group may also have valuable
23
24 314 information, such as knowledge of the location of a food source or a safe movement route
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26
27 315 (Couzin *et al.*, 2005). Benefiting from the knowledge and experience of conspecifics is
28
29 316 frequent in social insect movement (Rangel *et al.*, 2010). Animals travelling in a group can
30
31 317 also benefit from the presence of conspecifics by saving energy during movements, such as
32
33 318 formation flying in birds (Weimerskirch *et al.*, 2001), or schooling in fish (Herskin &
34
35 319 Steffensen, 1998), or by increasing time spent foraging through decreasing vigilance when
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37 320 foraging in a group (Krause & Ruxton, 2002). Group formation can also spread predation risk
38
39 321 across multiple individuals, enhance predator avoidance, or improve defensive strategies such
40
41 322 as the mobbing of predators (reviewed in Krause & Ruxton, 2002). On the other hand,
42
43 323 moving in groups involves costs such as increased competition for resources (Valone, 1989)
44
45 324 or slower movement if groups have to adjust their speed to the slowest individuals and
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47 325 consensus costs (Conradt & Roper, 2005). Groups can also be much more vulnerable to
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49 326 extrinsic threats like mortality from accidental events (Bleich & Pierce, 2001), and can also
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51 327 be easily detected and therefore vulnerable to exploitation (Sala, Ballesteros, & Starr, 2001).
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3 328 Synchronized settlement is well-documented in schooling larval fishes (Breitburg,
4
5 329 1989; Leis, 2006). Even in species with no schooling behavior at an adult stage, larvae of
6
7 330 several benthic fish species start schooling in a more or less advanced larval stage before they
8
9 331 settle (Leis, 2006). This schooling behavior during the transience and settlement phases
10
11 332 allows larvae to swim faster and in a straighter direction, as shown in the common
12
13 333 pomacentrid damselfish *Chromis atripectoralis* (Irisson *et al.*, 2015), and therefore may
14
15 334 reduce the high dispersal costs levied in such environments. Grouped individuals might also
16
17 335 achieve higher settlement success compared to lone individuals. When lone immigrants settle
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19 336 in an unfamiliar habitat, they might have difficulty finding resources (food, shelter),
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21 337 identifying potential risks (e.g. predators), or being accepted by locally resident individuals
22
23 338 (i.e. integration costs, Bonte *et al.*, 2012). The benefits of dispersal coalitions during
24
25 339 settlement have been well-studied in several cooperative species. Coalitions provide allies for
26
27 340 competition with unfamiliar individuals, increasing the likelihood of successful reproduction
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29 341 (Heinsohn *et al.*, 2000; Ridley, 2012). Interestingly, some social species display both solitary
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31 342 and coalition dispersal (Heinsohn *et al.*, 2000; Yano, 2008; Ridley, 2012), providing a
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33 343 promising model for evaluating the costs and benefits of the two dispersal modes.
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39 344 For example, the cooperatively breeding Arabian babbler *Turdoides squamiceps* can
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41 345 disperse both individually or in coalitions (Ridley, 2012). Interestingly, individuals typically
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43 346 disperse alone when moving into a group with a breeding vacancy, but may disperse as same
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45 347 sex coalitions when moving into a group where there is no breeding vacancy. Dispersing as a
46
47 348 coalition has costs, the main one being that after settlement the coalition breaks down and
48
49 349 typically only one individual becomes the dominant breeder, so that the others must disperse
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51 350 again. Coalition dispersal is, therefore, clearly not advantageous when breeding vacancies are
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53 351 available. However, the benefits outweigh the costs when dispersers must integrate into a
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55 352 saturated breeding group, evicting the residents. In this case, larger coalitions have a higher
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3 353 chance of evicting residents, while participating individuals loose less body mass as a result of
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5 354 dispersal costs. Individuals in the coalition, therefore, increase their own chance of becoming
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7 355 breeders. Interestingly, despite there being no evidence for dispersal polymorphisms, Ridley
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9 356 (2012) showed a high degree of individual repetability in solitary vs. coalition dispersal
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11
12 357 tactics.

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15 358 Similarly, the two-spotted spider mite *Tetranychus urticae* can disperse alone, either
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17 359 actively walking or being passively transported by other organisms or by wind (ballooning),
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19 360 or collectively, by forming silk balls that are transported by wind. Clotuche *et al.* (2011, 2013)
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21 361 recently elucidated some of the mechanisms and cost/benefit ratios involved in collective
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23 362 dispersal via silk balls. Typically, solitary dispersal is performed by mated females, while silk
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25 363 balls are mostly composed of immature individuals of both sexes. Moreover, the formation of
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27 364 silk balls seems to be triggered by food shortage and high population density. Passive
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29 365 dispersal, especially air-borne, has clear costs as the destination is completely out of the
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31 366 organism's control. Individuals have, therefore, a high chance of settling in unsuitable habitat.
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33 367 Additionally, when dispersing alone in areas where mates are not available or scarce,
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35 368 individuals settling in suitable habitat are prone to Allee effects. Clotuche *et al.* (2013) not
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37 369 only showed that silk balls mainly contain immature stages, but also that individuals do not
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39 370 segregate according to relatedness or sex. Moreover, silk balls help to reduce the risk of
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41 371 dessication during ballooning. However, silk balls also involve a high cost as individuals in
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43 372 the inner part of the ball usually die. Collective dispersal through silk balls seems, therefore,
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45 373 to be a good means for colonising new areas for this species, as the risk of Allee effects and
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47 374 inbreeding are reduced in newly founded populations.

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53 375 These two examples clearly exemplify how the balance between costs and benefits of
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55 376 solitary vs. collective dispersal depends on an individual's stage, phenotype and on social as
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57 377 well as ecological conditions. We might, therefore, expect the frequency of alternative tactics
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3 378 within a population to shift in response to changes in the environment that make collective
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5 379 dispersal more or less advantageous. For example, for the Arabian babbler, we might expect
6
7 380 more frequent coalition dispersal during severe climatic conditions (high cost of solitary
8
9 381 dispersal), or in highly saturated habitats (Ridley, 2012). In the same way, if the propensity
10
11 382 for collective dispersal has a strong genetic component, we might expect directional changes
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13 383 in ecological conditions to exert selective pressure to either increase or decrease the frequency
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15 384 of collective dispersal. For instance, in fragmented landscapes, dispersal costs are higher
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17 385 because dispersers are more visible to predators and the probability of finding a suitable
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19 386 habitat patch is lower (Bonte *et al.*, 2012). Hence, the occurrence and evolution of dispersal
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21 387 coalitions in these types of landscape should vary in relation to the costs and benefits of anti-
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23 388 predator defense (i.e. dilution and diversion effects vs. visibility to predators) and information
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25 389 gathering (i.e. amount of information vs. inaccurate information). Studies on recently
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27 390 fragmented or currently expanding populations, coupled with the development of eco-
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29 391 evolutionary theory on collective dispersal in fluctuating environments would be extremely
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31 392 useful to shed new light on when and where we should expect collective dispersal to evolve.
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37 393 (3) Spatial synchronization in transience and settlement

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39 394 Although temporal synchronization in dispersal appears to be virtually exclusive to
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41 395 social and marine species, spatial synchronization among dispersers might be more common.
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43 396 In some species, solitary dispersers follow the same dispersal path and settle in the same place
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45 397 as other members of the same initial population. Dispersal behavior has been shown to have
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47 398 both genetic and maternal determinants (Pasinelli, Schiegg, & Walters, 2004; Braendle *et al.*,
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49 399 2006; Sinervo *et al.*, 2006; Tschirren, Fitze, & Richner, 2007). In addition, siblings share the
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51 400 same birth location and the same potential destinations (Matthysen, Van de Castele, &
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53 401 Adriaensen, 2005) and are subject to the same maternal effects, including parental care
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55 402 (Matthysen *et al.*, 2010). Therefore siblings may disperse similar distances (Pasinelli *et al.*,
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3 403 2004) and/or in the same direction (Matthysen *et al.*, 2005), so that related individuals settle
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5 404 closer to each other than unrelated individuals (Matthysen *et al.*, 2005, 2010; Williams &
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7 405 Rabenold, 2005; Bernardi *et al.*, 2012). Independently of similarities in dispersal distance
8
9 406 and direction, kin may form aggregated settlements following dispersal as shown in ascidians
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11 407 (Grosberg & Quinn, 1986; Aguirre *et al.*, 2013). For instance, in the sessile colonial ascidian
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13 408 *Botryllus schlosseri*, larvae settle in kin aggregations and this settlement pattern cannot be
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15 409 explained only by dispersal distance (Grosberg & Quinn, 1986).

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18 410 Non-kin individuals might also display a degree of spatial synchronization in their
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20 411 dispersal behavior because individuals may use abiotic and biotic cues to locate suitable high
21
22 412 quality habitats including the location of conspecifics (Stamps, 2001). By doing so,
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24 413 individuals may benefit indirectly from the presence of conspecifics. Animals may be able to
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26 414 assess environmental quality through the presence of conspecifics without paying the costs of
27
28 415 detailed exploration. For example, Luschan's salamanders (*Lyciasalamandra antalyana*) use
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30 416 chemical scents deposited by conspecifics to identify a safe shelter (Gautier *et al.*, 2006).
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32 417 Using other individuals to assess environmental conditions is particularly useful in situations
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34 418 when animals have limited exploration capacity during migration or dispersal (Cote,
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36 419 Boudsocq, & Clobert, 2008). For example, individuals in several arthropod species follow
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38 420 tracks left by previous dispersers, using them as cues to identify potentially suitable dispersal
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40 421 trajectories (Yano, 2008; Fernandez, Hance, & Deneubourg, 2012). Similarly, intertidal
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42 422 gastropods are known to follow mucus trails left by conspecifics (Erlandsson & Kostylev,
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44 423 1995; Hutchinson *et al.*, 2007) and this trail-following behavior may explain similarities in
45
46 424 the direction of dispersal among individuals (Chapman, 1986). Dispersers may also use
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48 425 conspecific cues to select their new home range. In the gregarious tubeworm (*Hydroides*
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50 426 *dianthus*), larvae display a dispersal polymorphism, with a small proportion of larvae settling
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52 427 in uninhabited substrata while the majority settle in existing aggregations (Toonen & Pawlik,
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3 428 2001). This dispersal polymorphism has a significant genetic basis and is suggested to be
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5 429 maintained through a fitness benefit-cost balance. This mixed strategy, with a few asocial risk
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7 430 takers acting as colonizers and many social risk avoiders that join established colonies, may
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9 431 improve the speed of range expansion and invasion (Cote *et al.*, 2010; Fogarty, Cote, & Sih,
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11 432 2011). This type of spatially synchronized, but temporally distinct, collective movement
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13 433 seems to be widespread and not restricted to eusocial species. However, there is, to date, little
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15 434 empirical information available because studying such processes requires detailed monitoring
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17 435 of dispersal paths at the individual level, which is often difficult.
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23 437 (4) Spatial and temporal synchronization across dispersal steps

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25 438 The dispersal of semelparous organisms across regions, and even continents,
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27 439 particularly butterflies and moths, provides a clear example of extensive behavioral
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29 440 synchronization across the three steps of dispersal. Gene flow at this scale is dependent on a
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31 441 strong level of synchronization in departure, transience and settlement which underlies the
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33 442 multi-generational process required to achieve this fascinating coordinated dispersal of
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35 443 millions of individuals (e.g. Chapman *et al.*, 2015). However, as these specific examples
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37 444 have traditionally been considered within the evolutionary framework of migration, we will
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39 445 discuss them in section IV.
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43 446 Similarly, in marine species, synchronization of the entire dispersal process may
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45 447 occur, for example, when spawning is temporally and spatially limited or when it varies in
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47 448 relation to environmental gradients (e.g. Morgan, 1990; Hovel & Morgan, 1998). Collective
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49 449 dispersal, when kin or non-kin larvae that spawned at the same time are transported together
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51 450 and settle on the same site, is therefore likely, as suggested by the few available empirical and
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53 451 theoretical studies of this system (Selkoe *et al.*, 2006; Siegel *et al.*, 2008; Broquet *et al.*,
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55 452 2013). A few empirical studies further suggested that collective dispersal, from hatching to
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3 453 settlement, may result from active schooling behavior in marine larval fish (Bernardi *et al.*,
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5 454 2012; Ben-Tzvi *et al.*, 2012; Shima & Swearer, 2016).

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7 455 To conclude, because of the multiple determinants involved, dispersal is often
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9
10 456 perceived to be a solitary movement. However, it appears that temporal and/or spatial
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12 457 synchronization is less unusual than previously thought, at least for semelparous, social and
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14 458 marine species, and can even be observed unexpectedly in certain organisms. For example, in
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16 459 the nematode *Pristionchus pacificus*, larvae search for a new host by standing on their tail and
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18 460 waving their body to attach to a larger animal vector (Penkov *et al.*, 2014). Surprisingly,
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20 461 larvae produce an adhesive lipid that facilitates the congregation of multiple individuals into a
21
22 462 tall nematode tower-like structure. This waving tower probably maximizes the probability of
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24 463 attaching to a vector and results in collective host finding (Penkov *et al.*, 2014). With the
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26 464 exception of these intriguing examples, dispersal synchronization might be particularly more
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28 465 common for siblings, because they share both their environmental context (maternal and post-
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30 466 natal) and their genes.

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34 467 While eusocial species make up the majority of examples, synchronized dispersal also
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36 468 occurs in several other 'non-social' taxa. For example, in several aquatic species, larvae may
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38 469 undergo synchronized departure, transience and/or settlement. As in passively dispersing
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40 470 species, abiotic factors (e.g. wind and ocean currents) may result in the movement of a large
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42 471 part of the population in a synchronized manner. However, larvae may also actively school
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44 472 during transience or settlement, even though adults of the same species do not necessarily
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46 473 school (Leis, 2006). Collective dispersal may have evolved because of benefits similar to
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48 474 those obtained from grouping in other contexts such as feeding (e.g. reduced predation, better
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50 475 navigation and orientation) in social and non-social species while the costs of sociality may be
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52 476 higher than the benefits outside of the dispersal stage for non-social species. Aside from
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54 477 grouping benefits, synchronized movements may also result from sharing an abiotic or biotic

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3 478 vector in passively dispersing species (Fragoso, 1997; Nathan & Muller-Landau, 2000;
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5 479 Mazé-Guilmo *et al.*, 2016).
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8 480 III. SEASONAL MIGRATION

9 481 (1) Synchronization of departure

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12 482 Seasonal migration is a widespread behavior that enables animal populations living in
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14 483 highly seasonally variable environments to track spatio-temporal variations in suitable
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16 484 ecological conditions through the two-way movement of individuals back and forth between
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18 485 areas providing seasonally favorable environments (Lucas *et al.*, 2001; Alerstam,
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20 486 Hedenstrom, & Akesson, 2003; Milner-Gulland, Fryxell, & Sinclair, 2011; Avgar, Street, &
21
22 487 Fryxell, 2014). Seasonal migration provides some of the most striking examples of
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24 488 coordinated behavior in the animal kingdom, involving large numbers of individuals that
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26 489 move together through time and space in a synchronized fashion (Lucas *et al.*, 2001; Hubbard
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28 490 *et al.*, 2004; Hinch *et al.*, 2005; Milner-Gulland *et al.*, 2011). Although this kind of mass
29
30 491 migration is common, migration is in fact a diverse assemblage of movement types, including
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32 492 strongly spatially and temporally synchronized movements, solitary movements and partial
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34 493 migration, where only some individuals in a given population migrate (see references below).
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39 494 The benefits of migration clearly revolve around the exploitation of spatial and
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41 495 temporal variation in food availability, climatic conditions, predation risk, or a combination of
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43 496 several of these factors (Chesser & Levey, 1998; Boyle & Conway, 2007; Shaw & Couzin,
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45 497 2013; Avgar *et al.*, 2014). For instance, in marine and freshwater species, migration is
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47 498 defined as movements that result in an alternation between habitats used for reproduction,
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49 499 feeding or refuge with a regular periodicity within an individual's lifetime (Northcote, 1978;
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51 500 Lucas *et al.*, 2001; Binder, Cooke, & Hinch, 2011). All individuals of a given population
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53 501 should experience similar seasonal variation in conditions and should, therefore, initiate their
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55 502 migratory movement during a short time window. This underlies why migration is often
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3 503 defined as a synchronized movement of a large part of a population (Lucas *et al.*, 2001;
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5 504 Binder *et al.*, 2011). This temporal synchronization should be particularly strong when
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7 505 suitable environmental conditions for migration are temporally restricted (Duriez *et al.*,
8
9 506 2009). For example, arctic-nesting capital breeders have a narrow window for breeding which
10
11 507 might explain why spring migration is more synchronized than autumn migration back to the
12
13 508 wintering ranges (Madsen, Cracknell, & Fox, 1999). Furthermore, individuals generally do
14
15 509 not wait until environmental conditions deteriorate to leave because to do so may decrease the
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17 510 energy available for migration, and/or because late arrival at the wintering range may
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19 511 decrease their competitive ability (Alerstam *et al.*, 2003; Milner-Gulland *et al.*, 2011). For
20
21 512 example, some species migrate in order to track gradual changes in environmental gradients,
22
23 513 e.g. plant phenology for herbivorous birds and ungulates (i.e. surfing the green wave, Bischof
24
25 514 *et al.*, 2012; van Wijk *et al.*, 2012), rather than hopping between spatially distinct seasonal
26
27 515 ranges. This anticipation of changes in environmental conditions further intensifies the
28
29 516 temporal synchronization of departures within a given population. The initiation of migration
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31 517 should therefore be linked to early warning signs, or proxies, of habitat deterioration, or to an
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33 518 internal clock mechanism (Hinch *et al.*, 2005; Pulido, 2007; Ramenofsky & Wingfield,
34
35 519 2007). As a consequence, migration is facilitated by a variety of behavioral and physiological
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37 520 adaptations, also known as a migration syndrome, which may be under genetic and/or
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39 521 environmental control (Ramenofsky & Wingfield, 2007; Hedenström, 2008; Binder *et al.*,
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41 522 2011; Liedvogel, Åkesson, & Bensch, 2011). For example, diadromous fish migrating
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43 523 between seawater and freshwater environments display physiological adaptations to overcome
44
45 524 this osmoregulatory challenge (Hinch *et al.*, 2005). Another interesting adaptation is the
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47 525 ability to modify social behavior so that species which are usually territorial are able to form
48
49 526 large social groups for migration (Danilkin & Hewison, 1996; Alerstam *et al.*, 2003). For
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51 527 example, roe deer (*Capreolus capreolus*) males are strictly seasonally territorial, with very
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3 528 low levels of gregariness, and disperse as single individuals (Debeffe *et al.*, 2012), but in
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5 529 marginal parts of their range (e.g. Siberia), they migrate in large groups in a more or less
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7 530 synchronized mass long-distance movement (Danilkin & Hewison, 1996). Similarly,
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9 531 humpback whales (*Megaptera novaeangliae*), which are largely solitary, can be transiently
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11 532 involved in cooperative behaviors including migrating in small kin-biased groups (Valsecchi
12
13 533 *et al.*, 2002).

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16 534 The seasonal shifts in environmental conditions which initiate migration are, however,
17
18 535 not entirely predictable and may be largely gradual. As a result, there must be some flexibility
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20 536 in the migration syndrome (Ramenofsky & Wingfield, 2007; Binder *et al.*, 2011), which may
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22 537 explain intra-population variation in the timing of migration (Lucas *et al.*, 2001; Craig *et al.*,
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24 538 2003). For example, because the initiation of migration depends on social interactions,
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26 539 environmental cues and hormonal regulation, the timing of migration may vary among
27
28 540 individuals or classes of individuals (i.e. differential migration). Many migratory species
29
30 541 show some intra-population variation in migration timing which may reflect phenotypic
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32 542 variation driven by either genetic variation or differences in environmental conditions
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34 543 (Noordwijk *et al.*, 2006). For example, in southern German blackcap (*Sylvia atricapilla*),
35
36 544 migration traits (e.g. tendency, timing, distance) are heritable and a selection experiment
37
38 545 demonstrated that migratory strategies can be completely modified following two generations
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40 546 of selection (Pulido *et al.*, 2001; Pulido, 2007; Pulido & Berthold, 2010). Migration timing
41
42 547 may also vary over the lifetime or among life stages. For example, migration timing in
43
44 548 humpback whales varies with age, sex and reproductive status (Craig *et al.*, 2003). Within-
45
46 549 population differences in migratory traits can result in different migration patterns (Lucas *et*
47
48 550 *al.*, 2001). For example, in the roach (*Rutilus rutilus*), individual migrants vary consistently
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50 551 in the timing of their migration over multiple seasonal migratory events (Brodersen *et al.*,
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52 552 2012), while in bar-tailed godwits (*Limosa limosa baueri*) in New Zealand, individuals leave
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3 553 within the same week each year, resulting in high among-year repeatability of migration
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5 554 behavior (Battley, 2006).

6
7 555 An extreme **and widespread** form of intra-population variation in migratory behavior
8
9 556 is partial migration, where only a fraction of a given population migrates (Lundberg, 1988;
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11 557 Chapman *et al.*, 2011a). Partial migration has been **well**-documented in birds, mammals,
12
13 558 arthropods, amphibians and fish, providing clear examples of what could be considered as an
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15 559 extreme form of unsynchronized migration behavior (Lundberg, 1988; Hendry *et al.*, 2004;
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17 560 Chapman *et al.*, 2011a). The propensity to migrate may vary among **genotypes (Snyder,**
18
19 561 **1991; Lucas *et al.*, 2001; Páez *et al.*, 2011), among age, size or sex classes (Grayson &**
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21 562 **Wilbur, 2009; Páez *et al.*, 2011), or with local environmental conditions such as temperature,**
22
23 563 density, food availability or predation risk (Olsson *et al.*, 2006; Grayson & Wilbur, 2009;
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25 564 Griswold, Taylor, & Norris, 2011). Variation among individuals in competitive ability and/or
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27 565 vulnerability to predation may lead to the expression of distinct migratory strategies. For
28
29 566 example, Brönmark *et al.* (2008) developed a model to explore how a growth rate-predation
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31 567 risk trade-off could affect partial migration in roach. The winter migration of cyprinids from
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33 568 lakes to streams is explained by a higher ratio of predation risk to food availability (i.e. a
34
35 569 cost/benefit ratio) in the lake than in the streams during winter (Brönmark *et al.*, 2008).
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37 570 However, all individuals within a population are not equal with respect to vulnerability to
38
39 571 predators and foraging rate and this may explain observed inter-individual differences in
40
41 572 migratory behavior (Chapman *et al.*, 2011b). In elk of the Ya Ha Tinda herd near Banff
42
43 573 National Park, alternative migratory strategies are maintained: in comparison to resident elk,
44
45 574 migrant elk increase their reproductive success through access to higher forage quality, but at
46
47 575 the cost of lower survival due to wolf predation (Hebblewhite & Merrill, 2011). As a result,
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49 576 there is almost no difference in demographic performance between migratory and resident
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51 577 groups; hence the two tactics are maintained in the population.
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3 5784
5 579 **(2) Synchronization in transience and arrival**

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7 580 Dispersal typically involves an unknown destination, hence, synchronization in
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9 581 transience and settlement during dispersal are possible almost exclusively when departure is
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11 582 also synchronized. However, in long-lived iteroparous species, migration is often orientated
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13 583 towards the same location year after year, so that although migrants do not always leave
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15 584 together, they may converge en route or arrive at the same destination. Indeed, although
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17 585 migration commonly conjures up an image of large groups of individuals leaving their
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19 586 summer ranges together, travelling across the landscape as a single unit and arriving in their
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21 587 wintering areas together, synchronization of migratory initiation and transience may be
22
23 588 completely unconnected. For example, individuals that leave a given range separately may
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25 589 follow similar, or different, alternative migration paths, but arrive in the same wintering area
26
27 590 (Åkesson & Hedenström, 2007; Horton *et al.*, 2011). The migration of Siberian roe deer
28
29 591 typifies this case, where groups of various sizes leave their summer ranges in successive
30
31 592 waves over a period of about one month in early autumn. They then follow broadly similar
32
33 593 migration routes which are also consistently used from one year to the next, travelling over
34
35 594 100 km during 3-4 weeks, crossing major rivers at particular points, and finally settling in
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37 595 neighboring winter ranges (Danilkin & Hewison, 1996).

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39 596 The migratory path an individual takes will depend first on its orientation and
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41 597 navigational skills. Successful migration requires the ability to detect and interpret olfactory
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43 598 cues, the Earth's magnetic field, a sun compass and/or landmarks, abilities that are likely
44
45 599 genetically and/or culturally inherited (Lucas *et al.*, 2001; Alerstam *et al.*, 2003; Åkesson &
46
47 600 Hedenström, 2007; Binder *et al.*, 2011; Horton *et al.*, 2011). However, when migration is
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49 601 based on a more incremental tracking of suitable conditions, the ability to interpret
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51 602 environmental cues may be more important (van Wijk *et al.*, 2012). The speed an animal
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3 603 travels during migration also depends on its maximal locomotion speed, its rate of energy
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5 604 consumption/refueling and its ability to use external cues (Hedenström, 2008). Each of these
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7 605 traits may be under genetic and/or environmental control (Ramenofsky & Wingfield, 2007;
8
9 606 Åkesson & Hedenström, 2007; Binder *et al.*, 2011), so that the direction, speed and distance
10
11 607 of a migration event may vary within and between species and populations (Noordwijk *et al.*,
12
13 608 2006). First, individuals vary in their ability to deal with external factors (e.g. landscape
14
15 609 barriers, wind), with the result that they may move in different directions (Gschweng *et al.*,
16
17 610 2008). For example, in Northern wheatears (*Oenanthe oenanthe*), birds in good condition
18
19 611 migrate directly towards their breeding areas, crossing the sea, whereas birds in poor
20
21 612 condition migrate towards nearby mainland areas because of lower fuel availability
22
23 613 (Schmaljohann & Naef-Daenzer, 2011). Similarly, migrating individuals may choose their
24
25 614 stop-over sites in relation to the prevailing conditions in their habitat of origin (Végvári *et al.*,
26
27 615 2011). Second, independently of locomotion speed itself, migration speed also depends
28
29 616 strongly on fueling rate and energy consumption during locomotion, both of which may vary
30
31 617 with individual phenotype. Among-species comparison shows that migration speed and
32
33 618 distance is maximal in small-sized birds compared to large-sized birds, and this might also
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35 619 hold true among individuals within species (Alerstam *et al.*, 2003; Åkesson & Hedenström,
36
37 620 2007). These patterns may explain the degree of consistency in the duration of migration such
38
39 621 as that observed in greater snow goose (*Anser caerulescens atlanticus*; Bety, Giroux, &
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41 622 Gauthier, 2004). Finally, migration distance may also vary among individuals of a given
42
43 623 population, so that they choose different wintering or summering locations. This can result
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45 624 from variation in the direction and/or speed of migration. Six years of monitoring of roach
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47 625 migration showed that individuals had a consistently high level of site fidelity to their
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49 626 wintering ranges (Brodersen *et al.*, 2012). Indeed, migratory traits (timing, speed, distance,
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51 627 direction) often vary among individuals in a more or less consistent way (Bety *et al.*, 2004;
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3 628 Phillips *et al.*, 2005; Vardanis *et al.*, 2011; Brodersen *et al.*, 2012), so that asynchrony in
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5 629 migration behavior may persist at the population level. However, within the context of social
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7 630 information-based strategies (e.g. scroungers-producers), some individuals may rely more on
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9 631 the movement and navigational skills of others rather than on their own capabilities (Guttal &
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11 632 Couzin, 2010), thereby reinforcing temporal synchronization among migrants. For example,
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13 633 Guttal and Couzin's (2010) model predicted that individuals that use environmental cues
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15 634 during migration should be exploited by social information users.

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18 635 To conclude, seasonal migration has less labile drivers than dispersal, notably large
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20 636 scale and fairly predictable environmental shifts (e.g. seasonal cycles). The timing of
21
22 637 migration departure and arrival can have strong fitness consequences (e.g. on reproductive
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24 638 success). As a result, migration behaviors most often show a high degree of genetic
25
26 639 determinism (Pulido, 2007), although there are non-trivial levels of inter-individual variation.
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28 640 Together, these factors might explain why migratory movements are generally synchronized
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30 641 within groups of individuals, or even among different groups.
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35 36 643 **IV. SEASONAL MIGRATION AND DISPERSAL: INTER-CONNECTED** 37 644 **MOVEMENTS?**

38
39 645 Dispersal and seasonal migration are two large-scale movements which both involve
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41 646 an individual moving outside of its normal home range and/or natal site. This may be why
42
43 647 dispersal is sometimes referred to as a migratory strategy (Dingle & Drake, 2007; Chapman
44
45 648 *et al.*, 2015) and why these behaviors are often discussed together, creating some historical
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47 649 controversy (Kokko & Lundberg, 2001; Winkler, Greenberg, & Marra, 2005; Nathan *et al.*,
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49 650 2008).
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51 52 53 54 651 **(1) A teleological view of movement** 55 56 57 58 59 60

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3 652 Classifications of movements based on either *spatio-temporal scale* or *behavior* (see
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5 653 section I) are clearly not exclusive; nonetheless they represent different points of view that
6
7 654 have created decade long controversy in the field of the evolutionary ecology of large-scale
8
9 655 movements. One main source of misunderstanding stems from the fact that individuals and
10
11 656 species can have very *different strategies of space use* due to differences in their life-histories.
12
13 657 A useful distinction was proposed by Muller & Fagan (2008) who described three broadly
14
15 658 contrasted lifestyles: sedentary, migratory and nomadic. *Sedentary* individuals spend most of
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17 659 their lifetime in the same area (i.e. home range). In sedentary organisms, movements leading
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19 660 to gene flow (i.e., dispersal) are rare events in the lifetime of an individual and are dependent
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21 661 mainly on the social context. *Migratory* individuals generally occupy environments with
22
23 662 predictable seasonal fluctuations and perform regular, recurring long-distance movements
24
25 663 between spatially disjoint ranges. *Nomadic* individuals are not strongly faithful to any
26
27 664 particular range or area. Rather, they exhibit extremely long lifetime tracks (i.e. the
28
29 665 cumulative distance travelled by an individual during its life; Baker, 1978), continuously
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31 666 moving across the landscape in a non-regular fashion, mainly in response to highly
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33 667 unpredictable environmental conditions and/or resource distribution (Andersson, 1980; Allen
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35 668 & Saunders, 2002; Mueller & Fagan, 2008; Börger *et al.*, 2011; Jonzén *et al.*, 2011;
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37 669 Mueller *et al.*, 2011). Thus, the way in which foraging, dispersal and migration movements
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39 670 are expressed during the organism's life-cycle is clearly dependent on these three different
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41 671 lifestyles so that the definitions of these different movement types varies depending on the
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43 672 organism concerned. In particular, confusion arises when long-distance movements occur
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45 673 across generations, or for organisms which adopt the less well understood nomadic life-style.

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52 674 For example, in semelparous organisms (individuals that reproduce only once in their
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54 675 lifetime), some species display periodic changes in their distribution at the regional or
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56 676 continental scale as an evolutionary response to environmental degradation. The similarity of
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3 677 this process, typical of many invertebrates, and particularly well documented in insects (e.g.
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5 678 Chapman *et al.*, 2015), with seasonal migration has led to an alternative view of migration. In
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7 679 such organisms, the round trip is the result of a family affair: individuals that come back to
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9 680 the starting point of the “migration” process are the descendants of those that engaged in
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11 681 “migration” usually one or several generations before. Selection on migration should thus
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13 682 occur at the level of the group or deme. We suggest that a more evolutionary relevant
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15 683 explanation of the multi-generational movements of semelparous individuals should focus on
16
17 684 the relative costs and benefits at the individual level. In the northern hemisphere world-wide,
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19 685 butterflies and moths that overwintered in the southern part of the species’ distribution range
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21 686 fly northwards in spring, colonizing areas where hibernation is not possible due to the cold
22
23 687 climate. They mate and reproduce there, sometimes several hundred kilometers from their
24
25 688 departure point, and after development their offspring engage in the same kind of northwards
26
27 689 long-range movements. At mid-summer, when day/night length reaches a critical threshold,
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29 690 flight orientation is reversed and emerging adults and their subsequent offspring fly
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31 691 southwards to rejoin the southern part of the species’ distribution range in fall (e.g. Baguette,
32
33 692 Stevens, & Clobert, 2014; Chapman *et al.*, 2015). Such large-scale, oriented and multi-
34
35 693 generational movements occur also in the southern hemisphere worldwide, with inverse
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37 694 seasonality and flight directions. This pattern, involving millions of butterflies and moths (e.g.
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39 695 Chapman *et al.*, 2015), gives the impression of large scale movements comparable to
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41 696 enormous caribou or wildebeest herds migration. Although here gene flow is at the scale of
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43 697 regions or continents (Baguette *et al.*, 2014), at the individual level, there are no significant
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45 698 differences between this behavior of semelparous organisms (which has been referred to as
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47 699 migration) and the teleological definition of dispersal (movements potentially leading to gene
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49 700 flow, Ronce, 2007).

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3 701 Nomadic species also present a particular challenge in terms of definitions for their
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5 702 long-distance movements as they constantly move through the landscape in an unpredictable
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7 703 manner which is not repeated across time. It is broadly accepted that nomadism is an
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9 704 adaptation to environments with low productivity and a resource distribution which is highly
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11 705 variable and unpredictable in space and time (Mueller & Fagan, 2008; Jonzén *et al.*, 2011).
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13 706 However, it is not clear whether nomadism should be considered as a form of non-seasonal
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15 707 and undirected migration or a form of recurring breeding dispersal. In species/clades where
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17 708 individuals express several types of movements (Löfgren, Hörnfeldt, & Carlsson, 1986;
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19 709 Korpimäki, Lagerström, & Saurola, 1987; Mueller *et al.*, 2011), nomads may move over an
20
21 710 extremely large spatial scale (Mueller *et al.*, 2011), and these movements appear largely
22
23 711 driven by temporal variation in resources (Jonzén *et al.*, 2011). However, nomadic
24
25 712 individuals move in response to both environmental and social cues, most of which are still
26
27 713 poorly identified. These cues are likely more labile than the recurrent cues used by seasonal
28
29 714 migrants, so that a nomadic strategy is more plastic and less endogenously controlled (Jonzén
30
31 715 *et al.*, 2011), hence more akin to dispersal (Bennetts & Kitchens, 2000; Schwarzkopf &
32
33 716 Alford, 2002). Moreover, nomadic movements may involve either solitary individuals or
34
35 717 groups (see below). The main difference between the nomadic movements of groups and the
36
37 718 breeding dispersal movements that occur in sedentary species is that the whole group or
38
39 719 population moves together in space (Roshier & Reid, 2003). Although virtually nothing is
40
41 720 known about dispersal among social groups in nomadic species, both nomadism and dispersal
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43 721 always lead to some kind of gene flow, while migration does not necessarily do so.
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51 **(2) An evolutionary view of long-distance movements and their synchronization**

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54 723 Dispersal and seasonal migration have completely different ecological functions and
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56 724 evolutionary dynamics, with different ultimate and proximate causation. Indeed, although
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3 725 certain ecological factors may be implicated in both migration and dispersal (i.e. food
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5 726 availability, predation risk), these two types of movement have evolved in response to
6
7 727 different selection pressures: dispersal has evolved as a response to multiple drivers, notably
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9 728 kin interactions and inbreeding avoidance, intra-specific competition and environmental
10
11 729 stochasticity, whereas migration has evolved in highly seasonal environments in response to
12
13 730 large-scale and predictable spatio-temporal variation in ecological conditions. As a
14
15 731 consequence, individuals repeat migratory movements every year, while dispersal movements
16
17 732 occur occasionally over an individual's lifetime (except for nomadism). Therefore, even when
18
19 733 a given ecological factor drives the evolution of both migration and dispersal, the intensity
20
21 734 and nature of the selection pressure may often differ. For instance, the cumulative lifetime
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23 735 risk of predation should be higher for migrating than for dispersing individuals and may
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25 736 therefore drive stronger selection for group movements. From a proximate point of view,
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27 737 migratory strategies are believed to be mostly genetically determined and fixed (i.e.
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29 738 directionality, timing), whereas dispersal was traditionally considered as environmentally
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31 739 determined and plastic until the recent demonstrations of i/ significant heritability in this
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33 740 behavior (Zera & Brisson, 2012) and ii/ the existence of dispersal syndromes, i.e. suite of
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35 741 traits associated with different dispersal strategies, both among (Stevens *et al.*, 2014) and
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37 742 within species (Ronce & Clobert, 2012).

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44 743 However, despite these differences, the evolution of dispersal and migration may be
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46 744 inter-connected (Salewski & Bruderer, 2007), at least in part because they depend on the
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48 745 same locomotory systems. First, it has been hypothesized that dispersal was a precursor to the
49
50 746 evolution of migration (Salewski & Bruderer, 2007). When a species expands its distribution
51
52 747 through dispersal, it may colonize habitats where conditions are unsuitable for some parts of
53
54 748 the year. This may cause individuals to migrate back to the natal range after breeding in order
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56 749 to survive, returning only at the next breeding season. For example, in house finches
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3 750 introduced to the north-eastern USA, the proportion of migrants increased after introduction
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5 751 as the population extended its range (Able & Belthoff, 1998; Salewski & Bruderer, 2007).
6
7 752 On the other hand, asynchrony in migration may lead to some degree of gene flow (and so be
8
9 753 considered as a form of dispersal) in certain circumstances, and has even been hypothesized to
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11 754 be a driver of speciation. For example, in waterfowl, males may migrate to the breeding range
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13 755 of their female partners which can be spatially distinct from their original breeding range
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15 756 (Rodway, 2007), leading to gene flow. More generally, migrants may travel to a separate
16
17 757 breeding range because of navigational error and low homing precision. For example,
18
19 758 although homing precision in salmonids is generally higher than in non-salmonid species
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21 759 (Lucas *et al.*, 2001), a proportion of salmon fail to return to their natal rivers and are
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23 760 recaptured in nearby rivers, potentially driving the colonization of new habitats [(Quinn
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25 761 (1993) and Lohmann, Putman, & Lohmann (2008)].

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29 762 From our review, it appears that spatial and temporal synchronization during the three
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31 763 phases of dispersal (departure, transience and settlement) is not very widespread across taxa,
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33 764 and that synchronization during transience and settlement mostly occurs when departure is
34
35 765 also synchronized. In contrast, seasonal migration is one of the most striking examples of
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37 766 synchronized behavior in the animal world, although the degree of synchronization may vary
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39 767 across the different migration phases. Nomadism is particularly interesting in this respect, as it
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41 768 comprises both coordinated and uncoordinated movements, with differences among and
42
43 769 within species. Nomadic individuals move across the landscape along routes that can vary
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45 770 among individuals (type I nomadism; Mueller and Fagan 2008) or among years (type II
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47 771 nomadism; Mueller and Fagan 2008), depending on whether individuals are moving among
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49 772 multiple resource rich patches, or tracking a few resource patches. While the first type likely
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51 773 precludes coordinated movements among individuals (e.g. Bennetts & Kitchens, 2000;
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53 774 Schwarzkopf & Alford, 2002; Mueller *et al.*, 2011), the second type often leads to
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3 775 movement synchronization (Dean, 1997; Dorfman & Kingsford, 2001; McClure, Ralph, &
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5 776 Despland, 2011; Pedler, Ribot, & Bennett, 2014). For example, to track unpredictable broad
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7 777 scale variation in resources, nomadic Mongolian gazelles (*Procapra gutturosa*) move
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9 778 independently and in an uncoordinated manner (Mueller *et al.*, 2011). On the contrary, in
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11 779 arid and semi-arid environments in South Africa and Australia, nomadic bird species often
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13 780 move in groups of variable size (Dean, 1997; Pedler *et al.*, 2014), while in the nomadic
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15 781 caterpillar (*Malacosoma disstria*) movements are highly synchronized, with the entire colony
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17 782 travelling together (McClure *et al.*, 2011). This suggests that movement synchronization may
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19 783 mainly emerge in response to environmental drivers such as resource dynamics. However,
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21 784 collective movement and collective decision making (e.g., integration of information collected
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23 785 by many individuals) could also procure advantages for detecting and responding to highly
24
25 786 unpredictable and quickly changing pulses of resource availability (Jonzén *et al.*, 2011). For
26
27 787 example, from the foraging success of other individuals, conspecifics can obtain information
28
29 788 about habitat suitability (Valone, 1989), or find suitable travelling routes (Åkesson &
30
31 789 Hedenström, 2007). The so called ‘many-wrongs principle’ states that if each individual
32
33 790 makes their own, error-prone, assessment, but then tends to align with the direction of motion
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35 791 of others, environmental noise can be dampened due to multiple sampling by individuals
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37 792 within a group (Simons, 2004). Groups can also display an awareness of the environment
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39 793 which is not possible at the individual level. When local environment quality decreases,
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41 794 groups can respond to gradients that are impossible for an individual to perceive (Torney,
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43 795 Neufeld, & Couzin, 2009).

796 V. PERSPECTIVES

797 (1) Why does synchronization in dispersal matter?

798 There are multiple reasons that warrant spending greater effort on increasing our
799 understanding of synchronized dispersal behaviors, spanning from fundamental ecological

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3 800 and evolutionary theory, through consequences for population dynamics and genetic structure,
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5 801 to applications for better understanding and managing species' responses to environmental
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7 802 change.

8
9 803 First, collective dispersal behaviors are interesting in their own right. While above we
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11 804 have outlined the reasons why we should expect selection to favor collective movements in
12
13 805 certain contexts, we still lack a coherent picture of when and how we should expect
14
15 806 exceptions to this pattern. This ultimately boils down to understanding the benefits and costs
16
17 807 associated with these different types of movements. Hence, we could look at the problem
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19 808 from the opposing perspective, using these exceptions (if they really are exceptions) to better
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21 809 understand the selection pressures acting on dispersal and migration. Moreover, collective
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23 810 dispersal may be an important driver of the evolution of other social behaviors that are
24
25 811 difficult to explain such as, for example, altruism (Gardner & West, 2006). Interestingly,
26
27 812 understanding collective dispersal may also aid understanding of the evolution of mating
28
29 813 systems. For example, inbreeding avoidance is thought to be an important driver of dispersal
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31 814 (Perrin & Mazalov, 2000; Szulkin & Sheldon, 2008). However, from an inclusive fitness
32
33 815 point of view, certain levels of inbreeding could be beneficial to a degree that varies between
34
35 816 males and females (Kokko & Ots, 2006; Szulkin *et al.*, 2013). The balance between the costs
36
37 817 and benefits of inbreeding will influence the cost/benefit balance of dispersing together with
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39 818 relatives or as single individuals (Koykka & Wild, 2015).

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41 819 Second, collective dispersal has potentially important consequences for the
42
43 820 maintenance and structuring of genetic diversity within and among populations (Fix, 2004;
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45 821 Broquet *et al.*, 2013; Yearsley, Viard, & Broquet, 2013). Classic population genetic theory
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47 822 considers gene flow and hence dispersal as one of the major forces that reduces genetic
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49 823 diversity between populations and stabilizes allelic frequencies, counteracting micro-
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51 824 evolutionary local adaptation and genetic drift. However, studies focusing on collective
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3 825 dispersal, particularly when involving kin (“kin-structured migration”, Rogers, 1987; Fix,
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5 826 2004), have highlighted how kin dispersing in groups, as they are not a random sample of the
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7 827 source population, can actually increase genetic differentiation between neighboring
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9 828 populations so that significant local micro-evolutionary adaptation is not necessarily
10
11 829 precluded. These effects appear to be more likely in small populations with high dispersal
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13 830 rates. Hence, understanding when collective dispersal occurs and how dispersing groups are
14
15 831 structured in terms of inter-individual relatedness is important for the understanding of
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17 832 evolutionary processes and genetic structure across species’ ranges. In particular, considering
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19 833 the genetic effects of collective dispersal could be crucial for predicting outcomes in terms of
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21 834 range expansion and/or shift of species, as the colonization front is generally composed of
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23 835 small founder populations that often exhibit high dispersal propensity.
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27 836 The influence of collective movement on genetic structure and diversity also has
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29 837 important implications for inference regarding the process of dispersal. With a model focusing
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31 838 on neutral dynamics, Yearsley *et al.* (2013) showed that collective dispersal reduces genetic
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33 839 mixing between populations, which decreases expected coalescence times and increases
34
35 840 among-population differentiation (e.g. F_{ST}). This will affect estimates of dispersal rates and/or
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37 841 dispersal kernels inferred from genetic data. For example, high F_{ST} values, which would be
38
39 842 generally interpreted as a sign of low dispersal rates, could in fact be the result of high rates of
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41 843 collective dispersal (Yearsley *et al.*, 2013).
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45 844 Third, collective dispersal can play an important role in metapopulation and range
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47 845 dynamics. For example, perhaps intuitively, collective dispersal has been shown to be
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49 846 beneficial for metapopulation persistence in the presence of strong Allee effects (Fernandez *et*
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51 847 *al.*, 2012). In a simulation study on the dynamics of species invasion, Fogarty, Cote, & Sih
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53 848 (2011) included a sociability trait and found that a population consisting of social and asocial
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55 849 strategies had a higher chance of survival or expanding its range relative to a monomorphic
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3 850 population for either strategy. Hence, in some species, heterogeneity in personality, which is
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5 851 potentially linked to the propensity for collective movements (Johnstone & Manica, 2011),
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7 852 might be important for shaping the dynamics of species range expansions. Intriguingly, we
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9
10 853 may speculate as to whether recent environmental changes that force species to rapidly shift
11
12 854 their ranges might exert positive selection pressure not only for dispersal propensity to
13
14 855 increase, but also for dispersal behaviors to become more synchronized.

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16 856 Because of these potentially far reaching consequences of collective dispersal for both
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18 857 ecological and evolutionary processes, it seems clear that we should consider synchronization
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20 858 of dispersal as we build increasingly sophisticated models for predicting species' responses to
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23 859 environmental changes and for providing management recommendations, whether for
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25 860 conservation or containment of invasive species. However, before adding this complexity to
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27 861 predictive models, it is crucial that we first invest time and resources for developing
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29 862 underpinning theory and collecting high quality empirical data.
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33 34 864 **(2) Advancing theory on synchronized dispersal**

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37 865 Theory on collective movements of animals and, more broadly, on collective decision
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39 866 making and behaviors, has been gaining momentum over the past decade (Conradt & Roper,
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41 867 2005; Sumpter, 2010). This field has made exciting progress in advancing our understanding
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43 868 of mechanisms, proximate causes and ultimate evolutionary drivers of collective movements.
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46 869 Work has mainly focused on small spatio-temporal scale movements such as, for example,
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48 870 foraging, with the exception of some initial work done on migration (Guttal & Couzin, 2010).
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50 871 However, dispersal theory has yet to harness these advances, leaving an almost completely
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52 872 unexplored field of research: when should we expect individuals to take collective dispersal
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55 873 decisions and synchronize their dispersal behaviors? Below, we briefly highlight the main
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57 874 theoretical concepts on collective movements/decision making of animals and suggest
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3 875 possible ways in which these could be integrated with theory on the evolution of dispersal.
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5 876 Rather than focusing on how animals move together (for a review see Sumpter, 2010), we
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7 877 concentrate on why they do so and why collective movements are expected to emerge from
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10 878 individual behaviors or to evolve as a life history strategy.

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13 879 Theory on collective decision making deals with two fundamental points: the
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15 880 acquisition and sharing of information, and the resolution of conflicts of interest between
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17 881 individuals who have to converge towards consensual decisions in order to perform
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19 882 synchronized behaviors. A variety of theoretical models, most of which make use of game
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21 883 theory principles, have been formulated to address both issues and have been recently
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23 884 reviewed by Conradt (2011). Models considering information acquisition often ask which
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25 885 strategies of collective decision making are expected to maximize information accuracy and
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27 886 minimize the time taken to achieve the decision. In other words, given a degree of information
28
29 887 uncertainty, is it advantageous to take decisions as a group and, if so, which strategies of
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31 888 group decision making should we expect to evolve? Models include: i/ quorum responses
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33 889 (Sumpter & Pratt, 2009), which lead to a more accurate collective decision compared to a
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35 890 solitary decision, but at the cost of slowing the decision process; ii/ leadership models (Couzin
36
37 891 *et al.*, 2005), which have shown that once a certain number of individuals hold information,
38
39 892 other individuals can benefit from following the informed individuals without themselves
40
41 893 investing in information acquisition; iii/ independence-interdependence models (List,
42
43 894 Elsholtz, & Seeley, 2009), which have shown how the group can benefit from the pooling of
44
45 895 information acquired by multiple independent individuals; iv/ models of social parasitism,
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47 896 such as the producer-scroungers game (Sumpter, 2010), where some individuals invest in
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49 897 information acquisition (for example, food sources), while others exploit that information.
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56 898 Conflict models deal with situations where the balance between costs and benefits of
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58 899 achieving a collective decision, and hence performing a collective behavior, vary among
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3 900 individuals (Conradt & Roper, 2005; Conradt, 2011). Typically, these models consider cases
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5 901 where the optimal timing for initiating a particular behavior, or the optimal destination of a
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7 902 particular movement, differs among individuals or among sub-groups of individuals (e.g.,
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9 903 ages, sexes, physiological states). The magnitude and distribution of consensus costs among
10
11 904 individuals are particularly important (i.e., the cost of taking consensual decisions and
12
13 905 performing collective behaviors) relative to the benefits. Interestingly, it has been shown that
14
15 906 we should expect collective decisions to emerge more often for the initiation (timing) of a
16
17 907 particular movement, with predictions about leadership involving needs, physiological status
18
19 908 or personalities (Bazazi *et al.*, 2011; Johnstone & Manica, 2011), than for the movement
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21 909 destination (space). In the latter case, when consensus costs are high, we should expect either
22
23 910 dictatorial or solitary decision making to evolve (Conradt & Roper, 2009). As Sumpter
24
25 911 (2010) pointed out, collective behaviors, specifically movements in our case, can ultimately
26
27 912 be classified as coordinated and cooperative. Here, the assumption is that individuals move
28
29 913 because it is beneficial for them to do so, but coordination can emerge because a number of
30
31 914 individuals use the same environmental cues, or because some animals copy more informed
32
33 915 individuals. In contrast, cooperation should evolve as a result of the benefits of moving as a
34
35 916 group outweighing the costs. Game theoretic models that seek to explain the evolution of
36
37 917 cooperative movement/behaviors include social parasitism, mutualism, synergism, repeated
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39 918 interactions and altruism (Sumpter, 2010).

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46 919 These concepts have been applied by Guttal & Couzin (2010) in their individual-
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48 920 based, spatially explicit evolutionary model for the evolution of collective migration. In this
49
50 921 model, there are two evolving traits that determine individual fitness by accruing the costs and
51
52 922 benefits associated with migration: 'gradient detection ability' and 'sociality'. The 'gradient
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54 923 detection ability' trait determines an individual's ability to collect information about the
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56 924 environmental gradient it needs to follow to perform efficient migration. The 'sociality' trait

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3 925 determines the individual's tendency to be attracted to, and follow, other individuals. Both
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5 926 traits carry costs which increase monotonically with the trait values, and individuals
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7 927 reproduce with a probability that is proportional to the net cost-benefit balance determined by
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9 928 their strategy. Depending on the conditions and on the magnitude of, and balance between,
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11 929 the costs of the two traits, different strategies are predicted to evolve: residency (non-
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13 930 migration), solitary migration, collective migration in cohesive groups and collective
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15 931 migration resulting from fission-fusion dynamics initiated by a few leaders (Guttal & Couzin,
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17 932 2011). Collective migration evolves under a large range of conditions associated with
18
19 933 intermediate costs of sociality and gradient detection ability, and also at very low population
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21 934 densities where individuals would be expected to interact only rarely. Interestingly, when
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23 935 collective migration evolves, it includes two co-existing frequency-dependent strategies:
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25 936 "leaders" who have high gradient detection ability, but low sociality, and "social individuals"
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27 937 who have low or no gradient detection ability, but a high propensity for social interactions.
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29 938 Furthermore, at high levels of habitat fragmentation 'leader' strategies disappear, causing
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31 939 migration to be lost and, making it extremely difficult for a migratory strategy to reappear,
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33 940 even following habitat restoration.

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39 941 The commonalities between the body of theory briefly outlined above and dispersal
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41 942 behavior are remarkable but, from a theoretical point of view, still massively under-explored.
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43 943 Throughout the previous sections, we have highlighted the recent interest in 'informed
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45 944 dispersal' (Clobert *et al.*, 2009) and provided examples on how individuals rely on
46
47 945 environmental and social cues to take decisions at each stage of the dispersal process (Doligez
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49 946 *et al.*, 2002, 2003; Cote & Clobert, 2007a, 2010; Boulinier *et al.*, 2008; De Meester &
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51 947 Bonte, 2010). From the theoretical side, much work has been done on the evolution of
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53 948 density-dependent dispersal decisions, mainly focusing on emigration, where individuals'
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55 949 decisions on departure and/or settlement depend on information about the local density of
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3 950 conspecifics (Travis, Murrell, & Dytham, 1999; Travis *et al.*, 2009; Hovestadt, Kubisch, &
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5 951 Poethke, 2010; Poethke, Gros, & Hovestadt, 2011). However, relatively little attention has
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7 952 been paid so far to the role of information uncertainty (Schjorring, 2002; Bocedi, Heinonen,
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9 953 & Travis, 2012). Importantly, very little theory has been developed on how we should expect
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11 954 individuals to make use of information possessed by conspecifics at different stages of
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13 955 dispersal (Clobert *et al.*, 2009), whether and how we should expect individuals to follow
14
15 956 conspecifics, maybe evolving a form of social parasitism, and whether this could result in
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17 957 collective/synchronized movement behaviors at any of the three stages of dispersal. The
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19 958 model of Guttal *et al.* (2010, 2011) provides an excellent example of how the fields of
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21 959 collective movement, migration and evolutionary modeling can be integrated to obtain insight
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23 960 on the evolutionary dynamics of solitary vs. collective large-scale movements. Importantly, it
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25 961 also provides a first example of how this type of model could be used to understand if and
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27 962 how individual movement strategies matter for predicting a species' response to
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29 963 environmental change and, in turn, how environmental change may impact these strategies.
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35 964 Conflict models are particularly relevant for dispersal. In fact, much more so than for
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37 965 migration, dispersing individuals often have contrasting interests with regards to when and
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39 966 where to disperse. These conflicts arise as a consequence of the ultimate causes of dispersal.
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41 967 Individuals dispersing to avoid kin-competition might not want to settle together and compete
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43 968 with their kin for resources, hence, the decisions regarding whether or not to emigrate and
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45 969 where to settle should differ among kin. Similarly, if dispersal evolved as an inbreeding
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47 970 avoidance strategy, relatives of the opposite sex may have conflicting interests as to whether
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49 971 or not to disperse, as well as to when and where to disperse, leading, for example, to sex-
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51 972 biased dispersal. Both kin competition and inbreeding avoidance can exert contrasting
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53 973 selective pressures on different individuals, as the distribution of relatives in a population is
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55 974 likely to vary in time and space, and so be specific for a given individual. However, if
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3 975 dispersal evolved as a strategy to escape habitat deterioration, individuals might benefit from
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5 976 moving at the same time, pooling collective effort to find a suitable new habitat patch.
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7 977 Similarly, if populations are subject to Allee effects, moving together could facilitate group
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9 978 settlement, thereby mitigating the risk of reduced fitness due to low conspecific density. The
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11 979 prediction that collective decisions are expected to evolve more often for movement initiation
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13 980 than for movement destination seems to support the observation that collective decisions
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15 981 appear to be more prevalent during emigration than during settlement (see above). However,
16
17 982 the above prediction was not developed from models looking explicitly at dispersal. In reality,
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19 983 dispersal behaviors are likely to evolve in response to multiple drivers (Clobert *et al.*, 2012),
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21 984 making it challenging to predict whether or not group dispersal should be expected.
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23 985 Importantly, conflict models that wish to tackle these issues should incorporate these multiple
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25 986 drivers as sources of conflicting interests among individuals.
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30 987 Interestingly, the field of collective animal behavior and decision making has
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32 988 identified one of its future challenges as understanding how the outcome of evolutionary
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34 989 games for conflict decisions is influenced by information uncertainty (Conradt, 2011). In
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36 990 parallel, dispersal theory needs to move to the next level, integrating individual use of
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38 991 multiple sources of information with the multiple drivers of dispersal (Clobert *et al.*, 2009). It
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40 992 is therefore clear that a tighter interaction between the two fields could lead to mutual
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42 993 progress and aid understanding of when and where we should expect collective dispersal.
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44 994 Theory on synchronized dispersal evolution can further draw from what it is known about the
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46 995 density-dependence of synchronization in migratory behaviors. Partial migration, where only
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48 996 a part of the population migrates, is particularly interesting because it creates opportunity for
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50 997 frequency- and density-dependence of movement tactics. Most drivers of partial migration
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52 998 also depend on density (e.g. 5 out of 8 hypotheses in Chapman *et al.* 2011: competition for
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54 999 resources or breeding opportunities, predation risk and intraspecific niche diversity (Chapman
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3 1000 *et al.*, 2011a; Avgar *et al.*, 2014) and so does the frequency of migratory and resident tactics
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5 1001 (Kokko, 2011; Mysterud *et al.*, 2011). All the hypotheses that have been put forward to
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7 1002 explain partial migration (especially in mammals; (Avgar *et al.*, 2014), such as social fences,
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9 1003 competition avoidance or predation risk avoidance, are highly sensitive to population density.
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11 1004 Indeed, population density modulates the benefits and costs of social grouping and might thus
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13 1005 change the frequencies of migratory tactics. For example, a large scale monitoring of red deer
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15 1006 (*Cervus elaphus*) populations in Norway revealed negative density-dependence in the
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17 1007 proportion of migrants (Mysterud *et al.*, 2011), which tends to favor the social fence
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19 1008 hypothesis rather than competition avoidance. In turn, the frequency of migratory tactics may
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21 1009 suddenly alter local population densities. High frequencies of migrants leaving together may
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23 1010 push remaining residents to leave afterwards and eventually lead to the migration of the entire
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25 1011 population. Population density is also central to many theories on dispersal evolution;
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27 1012 however, no theory has looked at the potential effect of strong density-dependence on the
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29 1013 synchronization (especially temporal) of dispersal behaviors, or at how temporal
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31 1014 synchronization could in turn affect population density, hence feeding-back to the optimal
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33 1015 dispersal strategy.
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39 1016 **(3) Empirical studies: data collection and analysis**

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43 1017 The three phases of the dispersal process are rarely all monitored within a given study.
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45 1018 For example, researchers commonly observe the timing of dispersal departure (i.e.
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47 1019 emigration) and/or settlement (i.e. immigration), whereas transience is almost always
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49 1020 neglected. A major reason for this is the practical and technical difficulties of monitoring
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51 1021 movements of individuals over large spatial and temporal scales. Without detailed monitoring
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53 1022 of a sufficient number of individually recognizable animals across the three movement stages,
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55 1023 it is hard to ascertain whether individuals disperse on their own or as a synchronized group.
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3 1024 Previously, researchers had to rely on direct observation of individually recognizable animals
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5 1025 in areas where observability was high, for example, large ungulates and carnivores in open
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7 1026 plains (Holekamp, Boydston, & Smale, 2000), and/or repeated capture data of individually
8
9 1027 marked animals. Alternatively, movement synchrony is sometimes deduced where, following
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11 1028 movement, individuals are still associated with known members of their previous social unit,
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13 1029 which could imply that they dispersed together (Sharp *et al.*, 2008).
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17 1030 Dispersal studies would clearly benefit from adopting methods routinely used in
18
19 1031 migration and foraging studies (Lucas *et al.*, 2001). Sophisticated tracking devices have
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21 1032 become widely available, making it possible to accurately and precisely track individuals over
22
23 1033 large distances (Nathan *et al.*, 2003). This provides a promising avenue for obtaining
24
25 1034 information on movement synchrony during dispersal. Simultaneous GPS tracking of
26
27 1035 individuals may reveal unexpected social grouping or synchronized dispersal events (Lührs &
28
29 1036 Kappeler, 2013), although this does not provide information on the associated social context.
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31 1037 Indeed, spatial proximity does not necessarily imply coordinated behavior, although it is
32
33 1038 reasonable to assume that physical contact should increase as the frequency of close proximity
34
35 1039 events between pairs of individuals increases. Nonetheless, the frequency of interactions
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37 1040 among individuals is vital information for understanding the importance of the social context
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39 1041 of dispersal (Prange *et al.*, 2006). Combining telemetry data with information on social
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41 1042 interactions is likely to further improve our understanding of the mechanisms and drivers
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43 1043 behind the sociality of large scale movement.
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49 1044 Within the past decade, advances in technology have led to the development of
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51 1045 proximity loggers which can provide information on intra-specific interactions indexed by the
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53 1046 distance between individuals. Proximity loggers are electronic devices that both emit a unique
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55 1047 electronic signal and continuously monitor and record the time and duration of signals emitted
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3 1048 by other loggers (Prange *et al.*, 2006), enabling the detection of proximity between two
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5 1049 monitored individuals. One major advantage is that a threshold detection distance can be
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7 1050 defined, ranging from less than one to 100 m for logging encounters, with distance errors not
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9 1051 exceeding 3 m (Cross *et al.*, 2012). This system was primarily developed to study patterns of
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11 1052 space use among individuals (Atwood & Weeks, 2003), or location of predatory kills
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13 1053 (Tambling & Belton, 2009), but is increasingly used to measure and model contact rates for
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15 1054 questions of disease transmission (Hamede *et al.*, 2009), or group membership (Schauber,
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17 1055 Storm, & Nielsen, 2007). Because it provides continuous, individual-based, contact data
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19 1056 without requiring direct observation (Hamede *et al.*, 2009), this technology has tremendous
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21 1057 potential for understanding the sociality of dispersal. Currently, the weight and power
22
23 1058 autonomy significantly limit the applications of these systems, although some recent studies
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25 1059 on birds have been successful. For example, miniature proximity loggers have been used on
26
27 1060 Caledonian crow to establish a near real-time monitoring of association patterns (Rutz &
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29 1061 Troscianko, 2013). However, the use of proximity as a measure of inter-individual interaction
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31 1062 still does not provide any information regarding the type and duration of contact. Animal-
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33 1063 borne video and environmental data recorders (AVED) could provide information on the type
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35 1064 of interaction (i.e. the behavior of the performer, but also the response of the receiver) in
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37 1065 terms of social interaction during movement stages, as well as on environmental conditions
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39 1066 (Moll *et al.*, 2007). AVEDs have been used to study feeding habits (Newmaster *et al.*, 2013),
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41 1067 the use of tools (Rutz *et al.*, 2007), disease transmission (Lavelle *et al.*, 2012), and predation
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43 1068 (Loyd *et al.*, 2013). Further miniaturization (Rutz & Troscianko, 2013) and gains in energy
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45 1069 autonomy will increase the future applicability of this technology to a variety of model
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47 1070 systems. Coupling proximity loggers with miniature video cameras that are activated when
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49 1071 the individual is within a certain distance of a congener could be an energy-efficient way of
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51 1072 recording sociality during movement (Rutz & Troscianko, 2013).
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3 1073 **VI. CONCLUSIONS**

4
5 1074 1) Dispersal and migration are two conspicuous and superficially similar large-scale
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7 1075 movement behaviors. However, seasonal migrants are often thought to move together through
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9 1076 time and space in a synchronized fashion, while dispersers are believed to be solitary
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11 1077 individuals.

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15 1078 2) Our literature review shows that natal and breeding dispersal movements appear, for the
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17 1079 most part, to involve solitary animals. While it appears that temporal and/or spatial
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19 1080 synchronization is less unusual than previously thought, the vast majority of published
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21 1081 examples clearly concern semelparous and/or cooperative species. In contrast, migratory
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23 1082 movements are generally synchronized in time and space within groups of individuals, but
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25 1083 there are non-trivial levels of inter-individual variation in behavioral tactics.

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30 1084 3) The contrast in behavioral synchronization between dispersal and migration may derive
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32 1085 from differences in the selection pressures that drive their respective evolution. Indeed,
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34 1086 although certain ecological factors may be implicated in both migration and dispersal (i.e.
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36 1087 food availability, predation risk), dispersal has evolved as a response to multiple drivers,
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38 1088 notably kin interactions and inbreeding avoidance, intra-specific competition and
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40 1089 environmental stochasticity, whereas migration has evolved in highly seasonal environments
41
42 1090 in response to large-scale spatio-temporal variation in ecological conditions.

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46 1091 4) Although collective dispersal and solitary migration are seemingly rare, we still lack
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48 1092 enough information to rule these processes out as important components of some species eco-
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50 1093 evolutionary biology. Crucially, to date, there is hardly any theory developed for collective
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52 1094 dispersal: when should we expect to see it, why and how? Progress made on the theory of
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54 1095 collective animal movement, particularly regarding foraging, dispersal and, to a lesser extent,
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3 1096 migration, offers a promising way to move dispersal theory forward, especially with regard to
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5 1097 the use of social information by dispersing individuals and behavioral synchronization.
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9 1098 5) Understanding the occurrence and mechanisms of these collective behaviors can help us to
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11 1099 better understand the selection pressures acting on both dispersal and migration. Furthermore,
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13 1100 collective dispersal may have underappreciated and important consequences for species' eco-
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15 1101 evolutionary dynamics, affecting the evolution of other behaviors such as mating systems and
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17 1102 altruism, for the maintenance and structuring of genetic diversity within and among
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19 1103 populations and for metapopulation dynamics and range expansion. In particular, we still lack
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21 1104 a coherent picture of the role played by collective dispersal and of its possible evolution given
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23 1105 the novel selection pressures that currently prevail due to rapid global change.
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54 1118 **VIII. REFERENCES**

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1747 IX. SUPPORTING INFORMATION

1748 Additional supporting information may be found in the online version of this article.

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1749 **Table S1:** Data from published literature on collective dispersal.

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For Review Only

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3 1751 **Figure legend:**

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5 1753 **Figure 1:** Overview of the main ultimate and proximate causes of dispersal and migration

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7 1754 with the costs and benefits of collective movements. (a) Ultimate and proximate causes of

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9 1755 dispersal and migration and their effect on the expected degree of spatio-temporal

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11 1756 synchronization of the respective behaviors. For migration, strong genetic determination and

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13 1757 the fact that environmental cues are similar for all individuals, have low spatio-temporal

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15 1758 heterogeneity and high predictability, promote a high degree of synchronization (dark blue).

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17 1759 In contrast, for dispersal, the variety of proximate causes and the fact that they differ among

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19 1760 life-stages and that they exhibit high spatio-temporal heterogeneity and low predictability,

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21 1761 leads to a low degree of synchronization (light blue). However, proximate causes for dispersal

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23 1762 are likely to be similar for siblings, thereby promoting somewhat higher synchronization in

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25 1763 dispersal decisions among siblings. (b) Costs (purple) and benefits (green) of performing

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27 1764 collective behaviors/movements during dispersal and migration across the three stages of

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29 1765 departure, transfer and settlement. The arrows from a) to b) link the ultimate causes of

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31 1766 dispersal and migration with the costs and benefits of performing these behaviors collectively.

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33 1767 If dispersal evolves as a means of avoiding inbreeding, intra-specific and/or kin-competition,

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35 1768 we might expect collective dispersal not to be beneficial (purple arrows). However, in

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37 1769 cooperative species, budding dispersal (i.e. dispersing with kin) might simultaneously

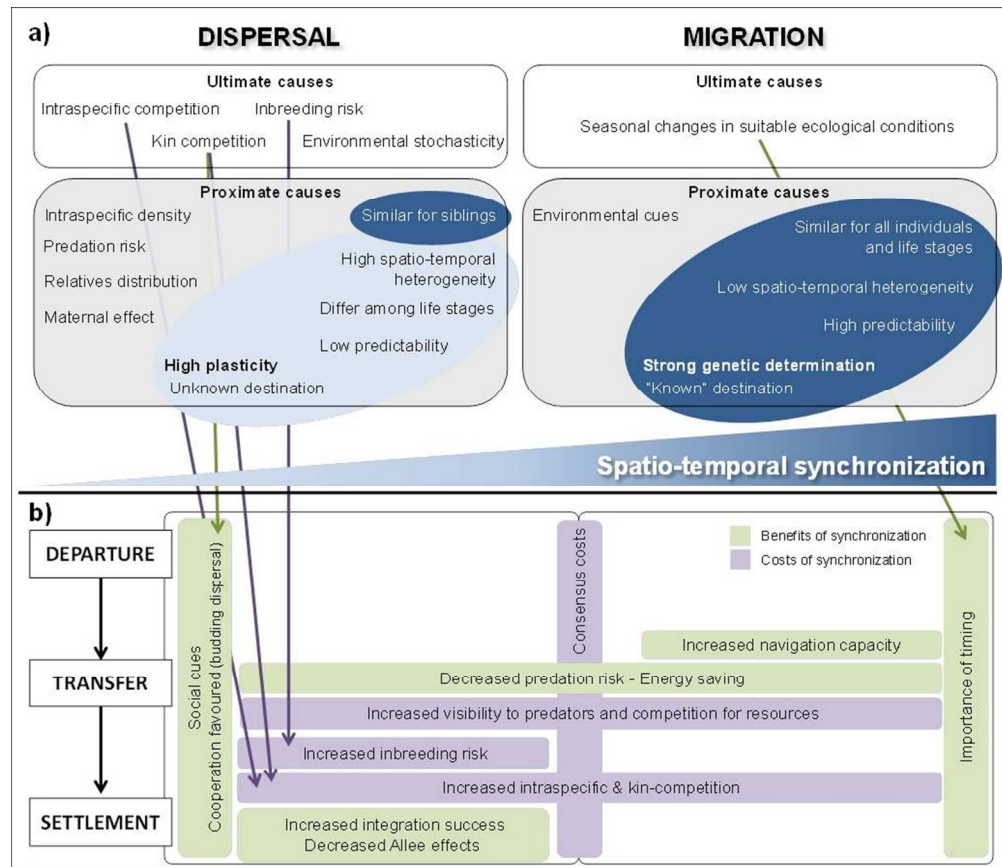
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39 1770 alleviate kin-competition and maintain the necessary level of relatedness for cooperation to

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41 1771 persist (green arrow). In contrast, migration mainly evolves as a response to seasonal changes

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43 1772 in suitable ecological conditions; thus, the timing of the different phases is likely to be crucial

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45 1773 for individual fitness and to act on all individual in similar ways, thereby promoting

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47 1774 synchronized behaviors (green arrow).
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36 Overview of the main ultimate and proximate causes of dispersal and migration with the costs and benefits
 37 of collective movements. (a) Ultimate and proximate causes of dispersal and migration and their effect on
 38 the expected degree of spatio-temporal synchronization of the respective behaviors. For migration, strong
 39 genetic determination and the fact that environmental cues are similar for all individuals, have low spatio-
 40 temporal heterogeneity and high predictability, promote a high degree of synchronization (dark blue). In
 41 contrast, for dispersal, the variety of proximate causes and the fact that they differ among life-stages and
 42 that they exhibit high spatio-temporal heterogeneity and low predictability, leads to a low degree of
 43 synchronization (light blue). However, proximate causes for dispersal are likely to be similar for siblings,
 44 thereby promoting somewhat higher synchronization in dispersal decisions among siblings. (b) Costs
 45 (purple) and benefits (green) of performing collective behaviors/movements during dispersal and migration
 46 across the three stages of departure, transfer and settlement. The arrows from a) to b) link the ultimate
 47 causes of dispersal and migration with the costs and benefits of performing these behaviors collectively. If
 48 dispersal evolves as a means of avoiding inbreeding, intra-specific and/or kin-competition, we might expect
 49 collective dispersal not to be beneficial (purple arrows). However, in cooperative species, budding dispersal
 50 (i.e. dispersing with kin) might simultaneously alleviate kin-competition and maintain the necessary level of
 51 relatedness for cooperation to persist (green arrow). In contrast, migration mainly evolves as a response to
 52 seasonal changes in suitable ecological conditions; thus, the timing of the different phases is likely to be
 53 crucial for individual fitness and to act on all individual in similar ways, thereby promoting synchronized
 54 behaviors (green arrow).

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