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1 The ability of individuals to assess population density influences the evolution
2 of emigration propensity and dispersal distance.

3

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23

24 **Abstract**

25 We analyze the simultaneous evolution of emigration and settlement decisions for actively
26 dispersing species differing in their ability to assess population density. Using an individual-
27 based model we simulate dispersal as a multi-step (patch to patch) movement in a world
28 consisting of habitat patches surrounded by a hostile matrix. Each such step is associated with
29 the same mortality risk. Our simulations show that individuals following an informed strategy,
30 where emigration (and settlement) probability depends on local population density, evolve a
31 lower (natal) emigration propensity but disperse over significantly larger distances – i.e.
32 postpone settlement longer – than individuals performing density-independent emigration.
33 This holds especially when variation in environmental conditions is spatially correlated. Both
34 effects can be traced to the informed individuals' ability to better exploit existing
35 heterogeneity in reproductive chances. Yet, already moderate distance-dependent dispersal
36 costs prevent the evolution of multi-step (long- distance) dispersal, irrespective of the
37 dispersal strategy.

38

39 Keywords: density dependent, kin-competition, distance-dependent dispersal cost,
40 metapopulation, individual-based model

41 **1. Introduction**

42 The evolution of dispersal is driven by the balance between dispersal related cost, e.g. the
43 mortality-risk during transitions or the energy and time spent on dispersal (Rankin and
44 Burchsted 1992, Zera and Denno 1997), and numerous potential benefits. These benefits
45 include avoidance of inter- or intraspecific competition for resources (Lambin et al. 2001,
46 Poethke and Hovestadt 2002), minimization of kin-competition (e.g. Hamilton and May 1977,
47 Comins 1982, Frank 1986, Comins and Hassell 1987, Rousset and Gandon 2002, Kisdi 2004,
48 Poethke et al. 2007) avoidance of inbreeding depression (Bengtsson 1978, Motro 1991, Perrin
49 and Goudet 2001) or coping with the temporal variability of resource availability (Levin et al.
50 1984, Travis and Dytham 1999, Gandon and Michalakis 2001). The possibility to colonize
51 new habitats, another benefit of dispersal, is critical for the persistence of a species (Alsos et
52 al. 2007).

53 So far theoretical studies on dispersal of actively moving organisms have mainly focused on
54 the emigration of individuals, while the dispersal process itself and the question how far to
55 disperse has been mostly ignored. Instead, the dispersal distance has been tackled with rather
56 arbitrary assumptions like nearest neighbour (e.g. Travis et al. 1999, Gros et al. 2006) or
57 global (e.g. Poethke and Hovestadt 2002) dispersal. The growing awareness of colonization
58 events through long-distance dispersal in plants (Nichols and Hewitt 1994, Nathan et al. 2002,
59 Bohrer et al. 2005, Nathan 2006, Alsos et al. 2007) has inspired the introduction and
60 investigation of “fat-tailed” dispersal kernels (Higgins and Richardson 1999, Bullock and
61 Clarke 2000, Hovestadt et al. 2001, Austerlitz et al. 2004, Katul et al. 2005) in theoretical
62 studies on seed dispersal. However, dispersal kernels describe the probability distribution of
63 dispersal distances away from a source. The use of dispersal kernels has thus mostly been
64 confined to studies of seed or pollen dispersal, or that of other organisms with passive
65 dispersal (Ezoe 1998, Gros et al. 2006) in continuous landscapes.

66 Although kernels have occasionally been estimated for actively moving animals (Baguette
67 2003, Gilbert et al. 2004, Chapman et al. 2007) and certain kernels are implicitly assumed in
68 metapopulation models (Hanski 1994), they appear inappropriate to capture the behaviour of
69 actively moving individuals. Such animals presumably do not leave habitat patches
70 accidentally (Van Dyck and Baguette 2005), but because of a decision to do so. Moreover,
71 they are believed to more or less continuously monitor the status of their surroundings during
72 movement (Nathan et al. 2008). It is likely that they can distinguish between suitable and
73 unsuitable habitat and can assess the expected benefit of further movement (Baker and Rao
74 2004). Habitat selection of actively moving animals has been object to several theoretical and
75 empirical studies (for a review see Morris 2003). Numerous examples show that animals react
76 not only to habitat quality but also on local population density (Morris 2010). For this reason
77 it is rational to consider dispersal of actively moving organisms as a three phase process with
78 different factors influencing decisions concerning i) emigration, ii) movement and iii)
79 settlement (Clobert et al. 2009).

80 When suitable habitat is patchily distributed and patches of habitat are embedded into an
81 environment unsuitable for reproduction, animals should continue their movement until they
82 find a suitable patch (Baker and Rao 2004, Stamps et al. 2005). In this case the realized
83 dispersal distance of individuals will crucially depend on the mean distance between patches
84 of suitable habitat (e.g. Hein et al. 2004). Yet, once dispersing individuals have discovered a
85 patch of suitable habitat, they may either settle or decide to continue their search for a new
86 breeding site. In this case, the final dispersal distance of actively moving animals will strongly
87 depend on their perseverance i.e. the probability to continue dispersal after having reached a
88 patch of suitable habitat. It is conceivable that an individual able to estimate the quality of its
89 natal site is also able to assess the quality of a site it has arrived in, and may consequently
90 continue to disperse if the quality of that site is perceived as too low.

91 We thus propose that dispersal distances should strongly depend on the capability of
92 individuals to use information on habitat quality in their dispersal decision whereas
93 uninformed dispersers should typically not continue dispersal once they have reached a new
94 potential breeding habitat. In the following we expand a previously published simulation
95 model (Poethke and Hovestadt 2002) to test this hypothesis. We compare the evolution of
96 dispersal distances for different degrees of spatial correlation in environmental conditions.
97 Local population density is a critical determinant of intraspecific competition and dispersal is
98 strongly motivated by the search for less populated habitats (Ruxton and Rohani, 1999, Travis
99 et al. 1999, Poethke and Hovestadt 2002). To account for organisms differing in their capacity
100 to assess local population density, we thus implement informed (in this case density
101 dependent) as well as uninformed (density independent) dispersal into the model and compare
102 the effect of either strategy on the evolution of dispersal.

103 More specifically, we test a number of hypotheses. (1) The number of successive dispersal
104 steps decreases with increasing dispersal costs (cf. Murrell et al. 2002). (2) The number of
105 dispersal steps increases with increasing spatial correlation in environmental conditions. With
106 increasing spatial correlation, animals have to disperse further to escape poor conditions (cf.
107 Frank and Wissel 1998, Murrell et al. 2002, Kallimanis et al. 2006). (3) Most importantly, we
108 test the hypothesis that short distance (that from the natal site to the first suitable site
109 encountered) dispersal prevails for uninformed dispersers, while dispersal events that cover
110 more than one step will only be found – in significant proportion – for the case of informed
111 (density dependent) dispersal.

112

113 **2. The model**

114 We use a modified version of the individual-based metapopulation model of Poethke and
115 Hovestadt (2002). The model simulates the population dynamics, inter-patch dispersal, and

116 the evolution of dispersal propensity in a meta-population of a diploid, sexually reproducing
 117 species with discrete generations and density-dependent local population growth. The
 118 metapopulation consists of habitat patches arranged in a square lattice of $24 \times 24 = 576$ cells. To
 119 avoid edge effects the metapopulation is closed into a torus (edges are wrapped). Each patch
 120 (i) supports a local population with carrying capacity $K = 40$; total carrying capacity of the
 121 system is thus ca. 23.000 individuals. Simulation experiments are initialised by placing K
 122 individuals in each of the 576 patches.

123 Within each patch populations grow according to a logistic growth model suggested by
 124 Hassell et al. (1976). Similar to Murrell et al. (2002) and Poethke and Hovestadt (2002), a
 125 female gives birth to $2 \times \lambda$ offspring where λ is Poisson distributed with mean $\lambda_{mean}(t, i)$. To
 126 account for environmental variability, $\lambda_{mean}(t, i)$ (specific for patch i at timestep t) is drawn
 127 from a log-normal distribution with mean $\bar{\lambda} = 2$ and a standard deviation of $\sigma = 1$.
 128 Offspring are randomly allocated to either sex. Offspring survival during maturation is
 129 dependent on the total number of offspring hatched in a patch (N_i). Thus, offspring mature
 130 with a density dependent survival probability s where $s = K_i / [K_i + (\bar{\lambda} - 1) \cdot N_i]$.

131 In all of our simulations, individuals are characterized by four alleles (n_1, n_2, f_1, f_2) at two
 132 diploid loci (n, f). The first of these loci (n) determines the individual's propensity for natal
 133 dispersal (P_n), the second (f) determines its perseverance, that is the probability (P_f) of
 134 continuing to disperse once it has successfully reached a suitable habitat patch. These alleles
 135 take continuous values and are initialised with uniformly distributed random numbers within
 136 the interval $[0.3, 0.5]$. Preliminary simulations showed that similar dispersal traits evolved
 137 independently of the starting values taken for initialising alleles (see appendix figure A2).
 138 Dispersal "decisions" can be either density-dependent (DD) or density-independent (DI). We
 139 performed simulation experiments for three different scenarios differing in the assumptions
 140 concerning the animals' capacity to perceive local population density and to adjust their

141 dispersal behaviour accordingly. In the first scenario (scenario DI_n/DI_f) natal dispersal
 142 propensity as well as perseverance, i.e. dispersal propensity for all further dispersal moves, is
 143 density-independent. In the second scenario (DD_n/DI_f) we assume that individuals can assess
 144 the population density in their natal patch, but do not have ability to assess the density of any
 145 patch they reach thereafter. Thus, natal dispersal propensity is density-dependent (DD_n) but
 146 perseverance is density-independent (DI_f). In the third scenario (DD_n/DD_f) all dispersal steps
 147 are density-dependent.

148 In the case of density independent dispersal, dispersal probability (the phenotype) is
 149 calculated according to the mean value of both alleles at the respective loci. This holds for
 150 density independent natal dispersal probability ($P_{DI,n} = (n_1+n_2)/2$) as well as for the
 151 probability to continue dispersal ($P_{DI,f} = (f_1+f_2)/2$) in the two scenarios with density
 152 independent perseverance (DI_n, DI_f and DD_n, DI_f).

153 In the case of density dependent natal dispersal, individual alleles do not determine the
 154 dispersal probability but a threshold density $C_n = (n_1+n_2)/2$ for dispersal. The actual dispersal
 155 probability $P_{DD,n}$ is then calculated according to the model derived by Poethke and Hovestadt
 156 (2002) as

$$157 \quad P_{DD,n} = \begin{cases} 0 & \text{if } C_i < C_n \\ 1 - \frac{C_n}{C_i} & \text{if } C_i \geq C_n \end{cases} \quad (1a)$$

158 Accordingly, the probability to continue dispersal in the case of density dependent
 159 perseverance (DD_n, DD_f) is calculated as

$$160 \quad P_{DD,f} = \begin{cases} 0 & \text{if } C_i < C_f \\ 1 - \frac{C_f}{C_i} & \text{if } C_i \geq C_f \end{cases} \quad (1b)$$

161 with $C_f = (f_1+f_2)/2$

162 For a full discussion concerning the adequacy of this model structure for density dependent

163 dispersal see Poethke and Hovestadt (2002) and Hovestadt et al (2010). It should be noted
164 that Ruxton and Rohani (1998) already utilized a model very similar to our DD_n/DD_f model
165 version to address questions concerning the stabilizing effects of dispersal on population
166 dynamics.

167 The three scenarios may correspond to three types of dispersers with different sensory
168 capacities. The first scenario (DI_n/DI_f) could apply to animals such as certain butterflies that
169 leave habitats independent of population density (e.g. Boughton 2000). The second scenario
170 (DD_n/DI_f) may apply to animals that acquire important information about population density
171 during their larval stage but disperse regardless of density as adults, such as e.g., migratory
172 locusts (Fuchs et al. 2003), or some crickets (Fowler 1988). In the third setting (DD_n/DD_f) we
173 assume animals that have the ability to assess local population density at any time. This most
174 likely applies to long-lived animals like mammals, birds, and a few insect species, e.g. some
175 corixid species investigated by Pajunen and Pajunen (2003).

176 For natal dispersal an individual randomly chooses one of eight neighbouring patches as
177 destination and then assesses successive patches along this trajectory thus keeping its
178 direction in each following step (see Figure 1). Dispersing individuals either reach the next
179 habitat patch or die during the transition with probability μ . Exploratory simulation runs
180 showed that individuals very rarely continued their dispersal for more than 10 consecutive
181 steps (see also results section), and we therefore limited the maximum number of movement
182 steps to 15. This had a negligible effect on simulation results but significantly reduced
183 computation time.

184 We modelled spatial correlation in habitat quality by aggregating patches into clusters and
185 assigning an identical value of $\lambda_{mean}(t, i)$ to all k patches within such a cluster. To account for
186 different spatial dimensions of correlation we vary the side-length of clusters from $l=1$
187 (cluster-size $k = 1$; no spatial correlation) to $l=4$ (cluster-size $k = 16$; see fig 1). Reproductive

188 conditions ($\lambda_{mean}(t, i)$) for each cluster were drawn anew every generation (t). The spatial
189 configuration of clusters does not change over time, so that each patch always belongs to the
190 same cluster.

191 When inheriting its parent's genes, mutations occur with a small probability ($m= 0.01$) per
192 allele. If mutations occur, the affected alleles are altered by adding a random value drawn
193 from a uniform distribution within the interval $[-0.1, 0.1]$. Preliminary simulation
194 experiments showed that an evolutionary equilibrium is usually reached after approximately
195 3000 generations (see appendix figure A2), yet each simulation run included 10000
196 generations. All results were recorded in the last generation. We varied stepwise dispersal
197 mortality μ as follows: $\mu = \{0.025, 0.05, 0.10, \text{ and } 0.20\}$.

198

199 **3. Results**

200 In all scenarios we find that uninformed dispersers (DI_n) evolve higher probabilities of natal
201 dispersal than informed dispersers (DD_n ; fig. 2a), whilst consecutive dispersal steps occur
202 with higher probability for informed dispersers (DD_f) than for uninformed dispersers (DI_f ; fig.
203 2b). Not surprisingly, natal dispersal probability (fig. 2a) as well as the mean number of
204 *additional* steps moved (fig. 2b) decreases rapidly with increasing dispersal mortality (μ). In
205 general, individuals are thus inclined to settle in the first patch they arrive in as soon as
206 dispersal mortality rises beyond even moderate levels ($\mu \geq 0.1$). The effect of dispersal
207 mortality on natal dispersal is more pronounced for the case of density independent natal
208 dispersal than for informed dispersal (fig. 2a).

209 Evolution of elevated natal dispersal probabilities for uninformed (DI_n , density independent)
210 compared to informed natal dispersal (DD_n) has already been described by Enfjall and Leimar
211 (2009) and Hovestadt et al. (2010): density dependent dispersal more efficiently exploits
212 inter-patch differences in population density, but also more efficiently homogenizes

213 population density across patches. To demonstrate this figure 3 compares the demographic
 214 benefits, that is, the mean difference in population size between the source and destination
 215 patch for the first five dispersal steps of emigrants. Evidently, the very first dispersal step is
 216 the most profitable one, i.e. is associated with the largest decline in pre- (natal patch)
 217 compared to post-dispersal (target patch) density. This holds for density dependent as well as
 218 for density independent dispersal. For example, with low dispersal cost ($\mu = 0.025$) and an
 219 accordingly high emigration probability, uninformed natal dispersers (DI_n/DI_f) arrive after
 220 their first dispersal step in a patch with on average 10.8 fewer competitors than in their natal
 221 patch (full dots, fig. 3a). If these individuals continue to disperse their second step will bring
 222 them to a patch with on average only 1.1 fewer individuals than their first target. With higher
 223 dispersal cost ($\mu=0.200$) emigration probabilities become generally lower but,
 224 correspondingly, the demographic benefits of natal dispersal increases (fig. 3b). Thus, with
 225 higher dispersal mortality ($\mu=0.200$) uninformed natal dispersers (DI_n/DI_f) arrive after their
 226 first dispersal step in a patch with on average 13.7 fewer individuals than in their natal patch
 227 (full dots, fig. 3b).

228 Informed dispersal allows a more efficient exploitation of inter-patch differences in
 229 population density. Even for the case of low dispersal cost (and relatively high emigration
 230 probability), density dependent natal dispersers (DD_n/DI_f and DD_n/DD_f) arrive in patches with
 231 on average 22.8 fewer individuals than in their natal patch (grey dots and open dots in fig. 3a).
 232 For the case of high dispersal cost ($\mu = 0.200$) the mean reduction in local population size
 233 achieved increases to 38.6 individuals (grey dots and open dots in fig. 3b).

234 The difference in the potential demographic benefit gained by dispersal between informed and
 235 uninformed strategies is not restricted to the first dispersal step: it is even more pronounced
 236 for the steps following natal dispersal. While the mean demographic benefit of a second
 237 dispersal step (i.e. the mean difference in population density between the target of their first

238 (natal) dispersal step and the target of their second step) for completely uninformed dispersers
 239 (DI_n/DI_f) is only 1.1 individuals (largely independent of dispersal cost, see filled circles in fig.
 240 3a and fig. 3b), completely informed dispersers (DD_n/DD_f) will realize a mean demographic
 241 benefit of 5.2 individuals in the case of low dispersal cost ($\mu = 0.025$; open circles in fig. 3a)
 242 and of 12.1 individuals for high dispersal cost ($\mu = 0.200$; open circles in fig. 3b) with a
 243 second dispersal step. Even those individuals that show informed dispersal in their first step
 244 but density independent dispersal in all other steps (DD_n/DI_f , grey circles) do profit slightly
 245 more from steps following natal dispersal than completely uninformed dispersers.

246 Natal dispersal equalizes population density to a considerable degree, thus reducing the
 247 potential benefits of further steps, while the costs for any such step remain the same.
 248 Consequently, even in scenarios with a rather benign cost of dispersal (e.g. $\mu=0.1$), only 2-5%
 249 of the emigrants take more than one dispersal step. With spatially correlated environmental
 250 fluctuations (figs. 3c and 3d) however, the demographic benefit for natal dispersal decreases
 251 while the benefit for all further dispersal steps increases. An increase in the demographic
 252 benefits gained by moving additional steps particularly emerges for individuals following
 253 uninformed secondary dispersal (for DI_n/DI_f compare filled dots in figs. 3a and b with figs 3c
 254 and d; for DD_n/DI_f compare grey dots in figs. 3a and b with figs. 3c and d) and it is largest for
 255 individuals that show density dependent natal dispersal but density independent dispersal in
 256 all other dispersal steps (DD_n/DI_f).

257 Spatial correlation has only a negligible effect on the probability of natal dispersal (fig. 4a)
 258 but the number of additional dispersal steps taken is strongly influenced by the spatial
 259 correlation in environmental conditions (fig. 4b); here we only show results for scenario
 260 DI_n/DI_f but results for the two other strategies are analogous (see appendix). At low dispersal
 261 mortality ($\mu=0.025$) the mean number of dispersal steps increases from 1.08 to 1.58 as cluster
 262 dimension increases from $k=1$ to $k=16$. Nonetheless, only 34% of all emigrants will continue

263 dispersal after the first dispersal step (see black dots in fig. A1). However, at a dispersal
264 mortality of $\mu=0.1$, the mean number of dispersal steps increases only from 1.02 to 1.05.

265

266

267 **4. Discussion**

268 The results of our evolutionary simulation experiments show that organisms with active
269 dispersal should typically settle into the first patch of suitable habitat they encounter, i.e.
270 disperse over short distances. Even for rather low levels of dispersal mortality individuals
271 hardly ever continue dispersal once they have reached a suitable patch. This supports the
272 findings by Barton et al. (2009), who modelled the (evolution of) movement rules of
273 organisms during transition. They found that organisms should target their movement to the
274 first (nearest) patch when patches become rare and movement in the matrix thus becomes
275 more costly. Selection for settlement in the first patch encountered particularly evolves for
276 uninformed dispersers and for spatially uncorrelated environmental conditions. Yet even in
277 spatially correlated environments density independent dispersers mostly settle in the
278 neighbouring patch as soon as step-wise dispersal mortality becomes moderate (e.g. $\mu \geq 0.1$).
279 Thus, most of these dispersers did not even leave the range of environmental correlation in the
280 scenarios with extended spatial clusters.

281 Under density dependent natal dispersal, the general tendency of individuals to leave the natal
282 patch decreases. However, at the same time, the average dispersal distance (number of
283 consecutive dispersal steps) is increased. Thus, the largest mean number of dispersal steps
284 recorded emerges for completely informed dispersal (DD_n/DD_f) in spatially correlated
285 landscapes. However, even in these scenarios, individuals typically move less than two steps
286 as soon as stepwise mortality risk becomes moderately large ($\mu \geq 0.1$).

287 As the costs for any dispersal step remain the same in our simulations, this decline in dispersal

288 probability must be attributed to a declining benefit of additional dispersal steps as the number
289 of steps increases. This declining benefit has two main causes: (1) Kin competition, a major
290 driver of dispersal (Hamilton and May 1977, Rousset and Gandon 2002, Poethke et al. 2007),
291 is already largely reduced with the first dispersal step, because siblings are spread over eight
292 neighbouring patches. Note that individual based simulation models of the evolutionary
293 process account for kin competition by default (Poethke et al. 2007). (2) The chance to reach a
294 habitat with fewer competitors decreases with every dispersal step simply because any round
295 of dispersal homogenizes population density ever further. The fact that spatial correlation has
296 little effect on natal emigration probabilities (see fig. 4a) despite the fact that demographic
297 benefits decline, supports the notion that this step is to a large degree driven by avoidance of
298 kin-competition. Only selection on taking further steps seems to be sensitive to demographic
299 benefits. The ability to control these latter benefits – moving from high- to low-density
300 populations – is responsible for the significant differences between informed and uninformed
301 dispersal strategies.

302 The evolution of elevated dispersal probabilities for uninformed (DI_n , density independent)
303 compared to informed natal dispersal (DD_n) can be traced to the fact that density dependent
304 dispersal more efficiently exploits inter-patch differences in population density, but also more
305 efficiently homogenizes population density across patches (Enfjall and Leimar 2009,
306 Hovestadt et al. 2010). This is the flip side of the larger demographic benefit achieved by
307 dispersing individuals following a density-dependent emigration strategy (fig. 3). Clearly,
308 homogenizing occurs most rapidly when the overall number of emigrants is large, i.e. when
309 dispersal mortality is low.

310 Only the DD strategy is adjustable in a way that allows ‘compensating’ increased dispersal
311 costs by also increasing the benefits as individuals emigrate only from especially densely
312 populated populations and thus collect especially large demographic fitness benefits *given*

313 they survive dispersal (Poethke et al. 2007). This explains the fact that under density-
314 dependent emigration natal dispersal is rarer, but consecutive dispersal steps occur with
315 higher probability.

316 Even when individuals disperse with a fixed probability (DI_n), more natal emigrants come, for
317 simple statistical reasons, from high density patches. Apart from the effect of kin-competition
318 (Hamilton and May 1977, Poethke et al. 2007), it is this simple truism that makes even
319 density independent natal dispersal a beneficial strategy in landscapes that exhibit spatio-
320 temporal variability in population density. For dispersal steps following natal dispersal this
321 argument does not hold however. Only immigrants, i.e. individuals that previously dispersed
322 already, are allowed to decide whether they want to continue dispersal or not, but a correlation
323 between population density and the number of immigrants no longer exists.

324 On the other hand, with completely density dependent dispersal (DD_n/DD_f) immigrants can
325 ‘recognize’ that they have arrived in a high-density patch and decide to move on. The
326 probability that this is indeed the case is supported by another mechanism already described
327 by (Hovestadt and Poethke 2006): under density dependent dispersal the distribution of the
328 number of emigrants becomes much more leptokurtic with occasional ‘mass emigration’ from
329 patches that have particularly good years. Such events also imply that large numbers of
330 individuals immigrate into the neighbouring patches. Consequently, dispersal itself creates a
331 spatial correlation in population density and makes it more profitable to continue dispersal
332 over several steps to leave the zone of correlation in population density. It is indeed this later
333 effect that explains why, rather surprisingly, the mixed strategy (DD_n/DI_f) also evolves higher
334 probabilities for consecutive dispersal steps. Due to the aforementioned effect, the recognition
335 of high density in the natal patch allows already predicting that, after the first ‘round’ of
336 dispersal, population density in neighbouring patches will be large too, even if individuals do
337 not have the ability to perceive the actual density there.

338 In our model we assume that individuals either have information on local population density
339 or not and that information acquisition is not costly. In real systems information acquisition
340 may come with a cost, e.g. as investment into sensual capabilities or into time needed for
341 information acquisition. Thus animals often use environmental cues (e.g. Stamps and
342 Krishnan 2005, Ichiki et al 2011) or information derived from the presence of heterospecifics
343 (e.g. Monikonen et al. 1999) to assess local habitat quality. Such indirect information will
344 necessarily be less precise. Thus, situations of intermediate information status will exist, too.
345 It requires further investigation to understand how information precision and investment into
346 its acquisition would affect the evolution of conditional dispersal strategies.

347 Despite the enormous interest of theoretical ecologists in the evolution of dispersal and its
348 ecological consequences, the great majority of studies on dispersal evolution have so far
349 focused on the evolution of dispersal propensity (e.g. Hamilton and May 1977, Janosi and
350 Scheuring 1997, Travis and Dytham 1999, Travis et al. 1999, Poethke and Hovestadt 2002,
351 Parvinen et al. 2003), while a smaller number of papers investigate the evolution of dispersal
352 distance (e.g. Ezoë 1998, Savill and Hogeweg 1998, 1999, Hovestadt et al. 2001, Murrell et
353 al. 2002, Rousset and Gandon 2002, Higgins et al. 2003, Muller-Landau et al. 2003,
354 Starrfelt and Kokko 2010, Travis et al 2010).

355 Usually the evolution of dispersal distances and the prediction of evolutionarily stable
356 dispersal kernels are analysed under the assumption of 'passive' and uncontrollable movement
357 as it occurs in seed dispersal, while investigating dispersal propensity has been a focus of
358 animal ecologists. At least in part this dichotomy is explained by the different mechanisms
359 that govern dispersal in plants and animals. In active as well as in passive dispersers, dispersal
360 incurs different types of cost. First, species that belong to either dispersal group must invest in
361 equipment that allows dispersal. This may be the flight apparatus of wind dispersed seeds
362 (Tackenberg et al. 2003), the elaiosome of ant dispersed seeds (Pfeiffer et al. 2010), the wings

363 and flight muscles of Orthoptera (e.g. Zera and Harshman 2001), or the silk thread of spiders
364 (e.g. Bonte et al. 2003). Such investment costs are paid once and are more or less independent
365 of the distance an individual will ultimately travel. However there are further costs that are
366 related to dispersal distance. With passive dispersal (especially in plants) the number of
367 propagules produced is typically large and dispersal is under maternal control. From the
368 perspective of a tree, it is the overall distribution of offspring that counts and it may pay in
369 evolutionary terms to allocate at least some offspring to risky long-distance dispersal. This
370 promotes the evolution of “fat tailed” dispersal kernels (Hovestadt et al. 2001; see also Roy et
371 al. 2001, Rousset and Gandon 2002, Starrfelt and Kokko 2010).

372 However, as explained in the introduction these approaches appear ill suited for the case of
373 actively moving organisms where the dispersal distances observed should be traced to the
374 interaction between landscape attributes and the rules governing the movement and especially
375 the settlement of organisms. Actively moving animals may continuously monitor their
376 surroundings (Getz and Saltz 2008, Nathan et al. 2008) and decide whether they continue to
377 move or stay once they have found a patch of habitat. At this moment the dispersing
378 individual may decide to either settle or move on. According to our results the tendency to
379 move on will clearly depend on the risk associated with searching for other suitable habitats
380 (cost of dispersal). In addition we would predict that species with well developed sensory (and
381 cognitive) abilities that are readily able to assess population density or habitat quality are
382 more likely to move on than species that do not have such abilities. On the other hand,
383 individuals that need much time (in relation to life-expectancy) or energy to collect such
384 information would typically settle in the first habitat they find.

385 Dispersal distance is an emergent property depending on behavioural rules on the one hand
386 and landscape attributes on the other (cf. Baguett and Van Dyck 2007). As ‘smart’ animals are
387 unlikely to settle just somewhere in the ‘matrix’ the distribution of dispersal distances will

388 strongly be defined by the typical distances between patches of suitable habitat. We believe
389 that our, certainly simplifying approach, is a useful step to better understand the evolution of
390 dispersal distances in actively moving organisms as an emergent property defined by
391 landscape attributes on the one hand and settlement rules on the other.

392 In summary we predict that with uninformed dispersal multiple dispersal steps should evolve
393 only if step-wise dispersal costs are rather low. Multiple dispersal steps are most likely to
394 evolve in species able to assess the quality of at least their natal habitat and in landscapes that
395 show strong spatial correlation of environmental conditions. However, as it presumably
396 requires time to collect information about habitat quality we expect that secondary dispersal
397 will most likely occur among long-lived species with considerable sensory and cognitive
398 abilities like mammals or birds.

399

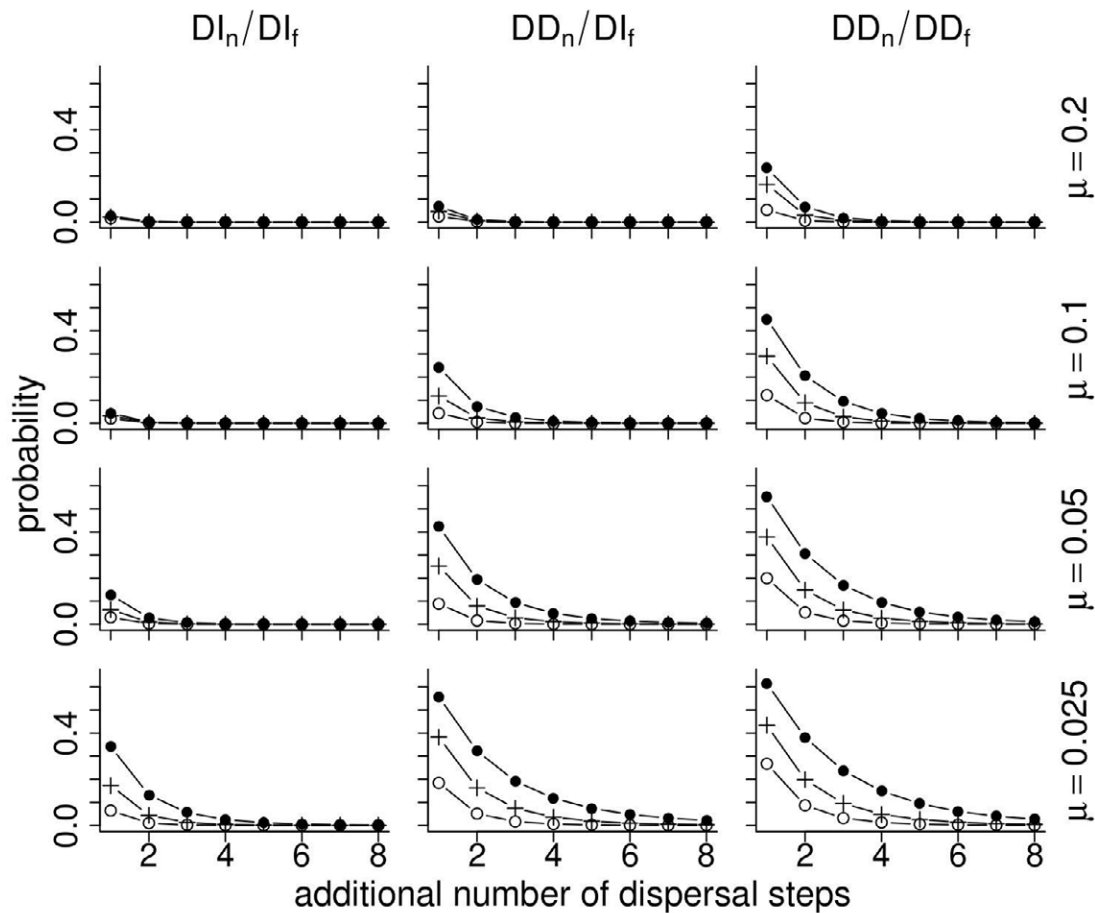
400 **Acknowledgements**

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405

406 Appendix

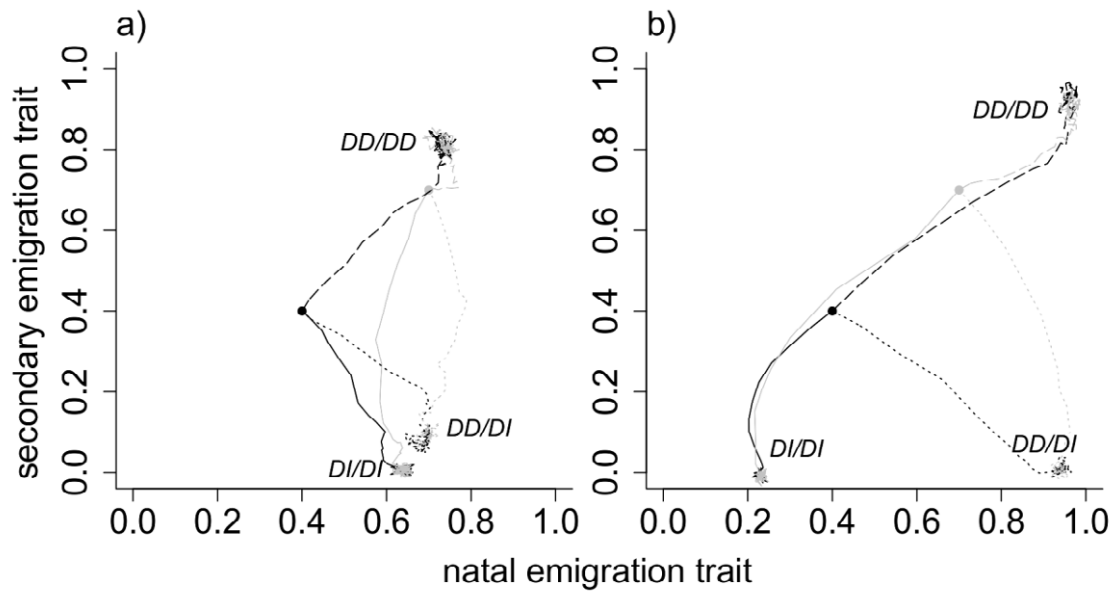
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408

409 **Figure A1**

410 Probability to perform at least n additional dispersal steps following initial natal dispersal,
 411 with n plotted on x -axis, as a function of dispersal cost (μ ; rows) and the mode of dispersal
 412 (columns). DI_n/DI_f : completely uninformed dispersal, DD_n/DI_f : density dependent natal
 413 dispersal but uninformed dispersal in all subsequent dispersal steps. DD_n/DD_f : completely
 414 density dependent dispersal. Different symbols reflect results for different scales of spatial
 415 correlation. Open circles: results for completely uncorrelated environmental conditions
 416 (cluster-size $k=1$), crosses for clusters of $k=4$ patches, and filled circles for clusters of $k=16$
 417 patches. In any generation, patches within same cluster are exposed to identical environmental
 418 conditions (λ_t).



419

420

421

422 **Figure A2**423 Exemplary plots of evolutionary trajectories for different dispersal mortalities (a: $\mu=0.05$ and424 b: $\mu=0.20$) and for each of the three different dispersal strategies investigated: DI_n/DI_f 425 (DI_n/DI_f (continuous lines), DD_n/DI_f (dotted lines), and DD_n/DD_f (hatched lines)). For each strategy we

426 initialized simulations at two different trait values for the two evolving traits (black and grey

427 dot). Note that the trait evolving is emigration probability for density-independent emigration

428 (DI) but the density threshold (C_n and C_f of equation 1) for density-dependent emigration

429 (DD). Emigration probabilities for the latter are shown in figures 2 and 4.

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609 **Figure Captions**

610

611 **Figure 1**

612 Symbolic representation of the landscape and dispersal behaviour of two representative
 613 individuals. Circles represent patches of suitable habitat, the space in between the hostile
 614 matrix. Clusters of circles of similar shading represent clusters of patches with similar
 615 environmental conditions (for this case $4 \times 4 = 16$ patches per cluster). Thin arrows depict
 616 possible dispersal moves during natal dispersal of a focal individual (nearest neighbour
 617 dispersal). For natal dispersal an individual chooses a direction at random (fat arrow) and in
 618 the following steps it keeps this direction (broken arrows).

619

620 **Figure 2**

621 Influence of dispersal mortality (μ) on natal emigration probability (a) and the mean number
 622 of steps an emigrant takes (b), for uninformed dispersal (DI_n/DI_f ; filled circles), density
 623 dependent natal dispersal but density independent dispersal for any subsequent dispersal steps
 624 (DD_n/DI_f ; grey circles), and completely density dependent dispersal (DD_n/DD_f ; open circles).
 625 Result of simulation experiments in worlds of 576 patches of capacity $K = 40$ with
 626 uncorrelated environmental fluctuations (cluster-size $k = 1$).

627

628 **Figure 3**

629 Mean stepwise difference in population density between start- and target-patch for the first
 630 five consecutive dispersal steps of dispersing individuals following different dispersal
 631 strategies (DI_n/DI_f = filled circles; DD_n/DI_f = grey circles; DD_n/DD_f = open circles). Left
 632 column (a, c) gives results for low dispersal mortality ($\mu = 0.025$), and right column (b, d) for
 633 high dispersal mortality ($\mu = 0.200$). Upper row (a, b) gives results for uncorrelated (cluster-

634 size $k = 1$) lower column (c, d) those for correlated (cluster-size $k = 16$) environmental
635 conditions. Result of simulation experiments in worlds of 576 patches of capacity $K = 40$. In
636 any generation, patches within same cluster are exposed to identical environmental conditions
637 (λ_t) .

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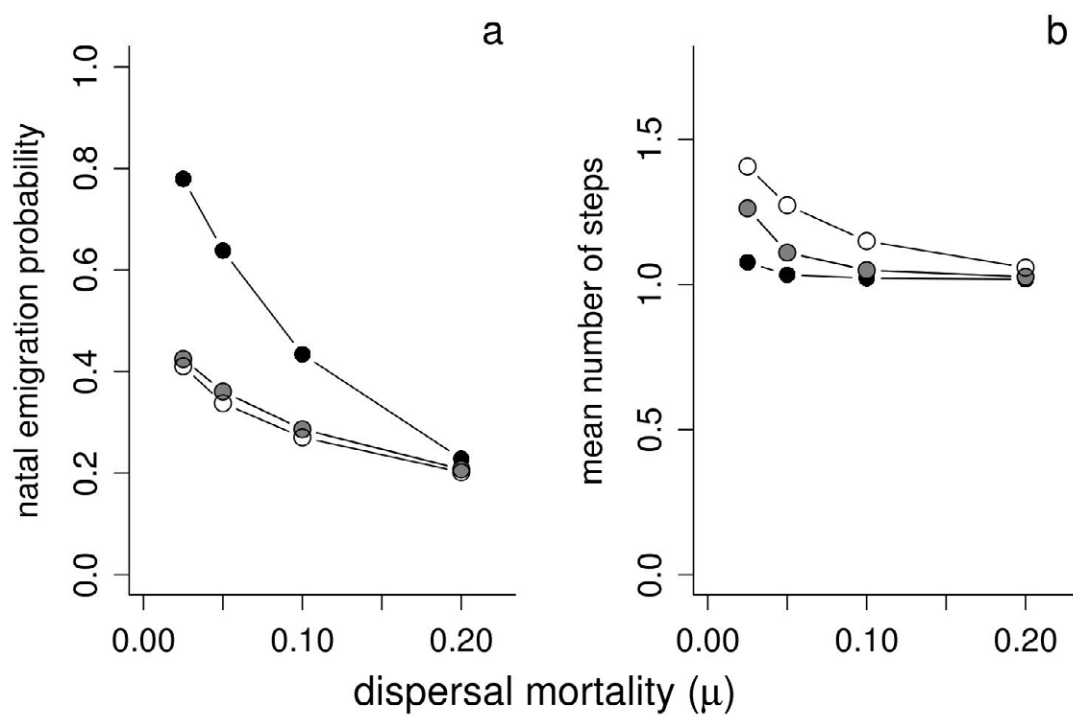
639 Figure 4

640 Influence of dispersal mortality (μ) on natal emigration probability (a) and the mean number
641 of steps an emigrant covers (b) for completely uncorrelated worlds ($k=1$; filled circles),
642 spatial correlation distance $l=2$ ($k = 4$; grey circles) and spatial correlation distance $l=4$ ($k =$
643 16 ; open circles). Result of simulation experiments with density independent dispersal
644 (DI_n/DI_f) in worlds of 576 patches of capacity $K = 40$. In any generation, patches within same
645 cluster are exposed to identical environmental conditions (λ_t) .

650 Figure 2

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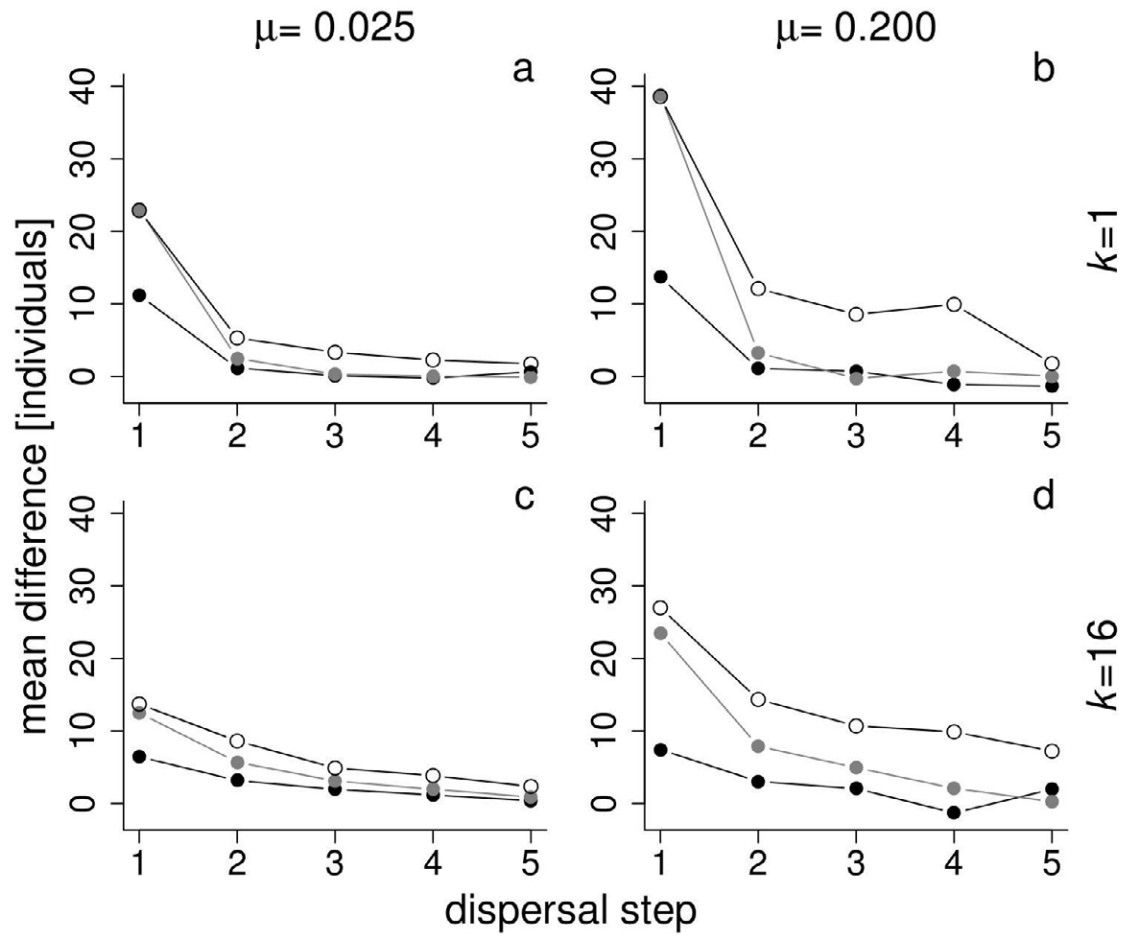
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655 Figure 3

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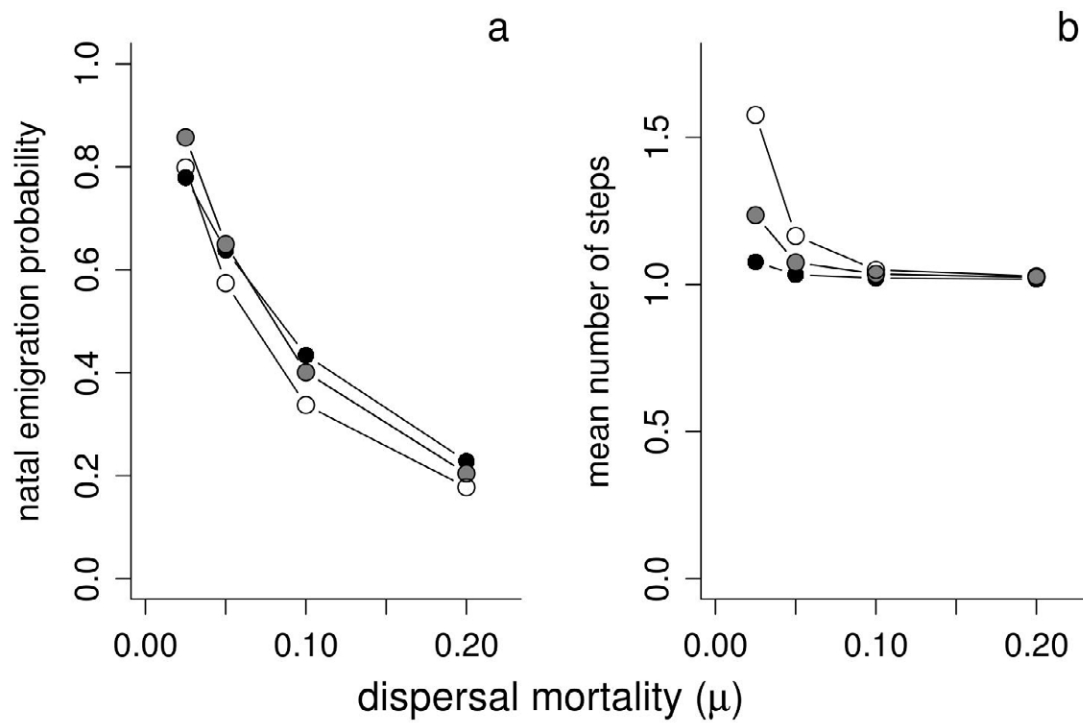


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661 Figure 4



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Accepted manuscript