Information Transfer Across Landscapes and the Co-evolution of Multiply-Informed Dispersal from Neighbors and Immigrants

Dispersal plays a key role in natural systems by shaping spatial population and evolutionary dynamics. Dispersal has been largely treated as a population process with little attention to individual decisions and the influence of information use on the fitness benefits of dispersal despite clear empirical evidence that dispersal behavior varies among individuals. While information on local density is common, more controversial is the notion that indirect information use can easily evolve. We used an individual-based model to ask under what conditions indirect information use in dispersal will evolve. We modeled indirect information provided by immigrant arrival into a population which should be linked to overall metapopulation density. We also modeled direct information use of density which directly impacts fitness. We show that immigrant-dependent dispersal evolves and does so even when density dependent information is available. Use of two sources of information also provides benefits at the metapopulation level by reducing extinction risk and prolonging the persistence of populations. Our results suggest that use of indirect information in dispersal can evolve under conservative conditions and thus could be widespread.

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13   **INTRODUCTION**

15   Dispersal is a key component of many ecological and evolutionary processes ranging

16   from population dynamics to local adaptation and has been the focus of extensive empirical and

17   theoretical investigation (Clobert et al. 2001; Ronce 2007; Nathan et al. 2008; Clobert et al.

18   2012). The impact of dispersal on both population dynamics, movement across the landscape,

19   and local adaptation makes it a critical element of understanding how populations are affected by

20   landscape fragmentation and global warming (Chaine & Clobert 2012). Dispersal has largely

21   been treated as a population level character even though dispersal decisions are fundamentally an

22   individual behavior that should benefit from knowledge of the landscape. Recent empirical

23   evidence suggests that information use in making dispersal decisions and navigating the

24   landscape plays an important role in patterns of dispersal (Bowler & Benton 2005; Clobert et al.

25   2009; Schmidt, Dall & Van Gils 2010). Information use would cause a shift in how we view

26   dispersal. Exchanges among populations would no longer represent a random subset of

27   genotypes and might affect local adaptation patterns. Dispersers might not spread randomly

28   across the landscape and some populations might receive more or fewer immigrants. In applied

29   work, if we want to encourage dispersal, we would need to make sure that the key information

30   sources are available or even manipulate information to get the desired level of dispersal. Yet our

31   fundamental understanding of informed dispersal remains limited (Clobert et al. 2009).

32   The use of information in dispersal decisions has received attention through a limited

33   range of possibilities despite potentially important effects on fitness (Ims & Hjermann 2001;

34   Ronce et al. 2001; Bowler & Benton 2005; Clobert et al. 2009; Schmidt et al. 2010). Classical

35   ecological (metapopulation) and evolutionary (gene-flow) theory assumes constant dispersal

36   rates with more or less random movement and no information use (Hanski & Gaggiotti 2004). At

37   the other extreme, ideal free settlement models assume perfect knowledge of the entire landscape

38   which influences dispersal (Holt & Barfield 2001). Both approaches are analytically tractable,

39   but biologically unrealistic since organisms often use some information but rarely have perfect

40   information. Significant progress in understanding dispersal itself will require specific attention

41   to biologically plausible mechanisms for gathering information (Schmidt et al. 2010).

42   Recent models have investigated how local population density affects dispersal (Travis,

43   Murrell & Dytham 1999; Cadet et al. 2003; Ronce 2007; Enfjäll & Leimar 2009; Hovestadt,

44   Kubisch & Poethke 2010; Bocedi, Heinonen & Travis 2012), but it is becoming increasingly

45   clear that organisms use a variety of information sources (Ronce et al. 2001; Danchin et al. 2004;

46   Bonnie & Earley 2007; Clobert et al. 2009; Schmidt et al. 2010) that might inform them about

47   the presence or content of other populations in the landscape. For example, tourists in Paris are

48   easily identified by the fact that they are using maps (unlike Parisians) and this suggests that

49   there is indeed a habitable world outside of Paris. These more 'indirect' sources of information

50   derived from the observation of conspecifics are more controversial because they less accurately

51   predict fitness in any given patch (Schmidt et al. 2010). However, indirect information carries a

52   distinct advantage of providing some information about other patches without requiring costly

53   exploration of other sites. A few recent empirical examples in birds, lizards, and other organisms

54   now suggest that indirect social information is accessible and used by individuals in making

55   dispersal decisions (Doligez, Danchin & Clobert 2002; Cote & Clobert 2007a; Chaine et al.

56   2010; De Meester & Bonte 2010). Yet it remains unclear how prevalent this behavior might be

57   across species. Widespread use of indirect information would dramatically alter our

58   understanding of dispersal and would have consequences for both fundamental work in ecology

59   and evolution as well as applied conservation.

60   Using a theoretical model, we show that simple rules for the use of indirect social

61   information in dispersal decisions can evolve under a broad range of conditions and therefore

62   might be quite common in nature. We investigated the evolution of information use prior to

63   dispersal using a simple metapopulation model in which we allowed information use in dispersal

64   to evolve. We were primarily interested in whether the use of indirect information provided by

65   immigrants could evolve, and if so, could it evolve in competition with direct information about

66   local density.

67

68   **THE MODEL**

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70   We constructed an individual-based model of informed dispersal behavior, based on

71   information about the local density and/or the number of immigrants, while simplifying the

72   landscape and genetic features of the system. In each patch, discrete time structured population

73   dynamics were modeled using a two age class life cycle with age-specific demographic

74   parameters (Fig. 1). Our initial model used a 'fast' life history roughly equivalent to a small

75   lizard or passerine life cycle (survival: $s_0=0.2$, $s_1=0.35$, $s_2=0.5$; fecundity: $f_1=7$, $f_2=7$). Juveniles

76   were given the opportunity to disperse to other patches prior to the subsequent reproductive

77   episode if they survived their first year. All patches were equally connected and population size

78   was limited at reproduction by the maximum patch carrying capacity which was the same for all

79   patches ($K=100$). This configuration leads to very stable populations with low levels of

80   demographic stochasticity and very small benefits of dispersal (populations are all similarly near

81   *K*) essentially creating a conservative scenario for the evolution of informed dispersal.

82   The simulation was in discrete time. Individuals were described by their age, the values

83   of their adaptive traits (see below), their patch of residence, their dispersal status, the strategy

84   they played if they dispersed, and the probability of dispersal. At each time step, the following

85   operations are performed in sequential order for all individuals in the metapopulation: Survival;

86   Reproduction and mutation; Dispersal.

87   We modeled two forms of information use that could influence dispersal: 1) measures of

88   the local density which are known to provide a benefit to dispersal behavior (Cadet et al. 2003)

89   and 2) measures of the number of immigrants entering a patch (Cote & Clobert 2007a). Local

90   density directly influences reproductive success whereas the number of arriving immigrants

91   indicates that other populations are attainable and may provide some information about overall

92   metapopulation density. The influence of local density and immigrant-borne information on

93   dispersal behavior were modeled as:

94

95   Density-dependent: $D\dfrac{n_i}{K_i} - 2$ (1)

96

97   Immigrant-dependent : $\mathfrak{I}_i - 2$ (2)

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99   where n_i is the number of individuals in patch *i*, $K_i = K$ is the patch carrying capacity, and M_i is

100   the number of immigrants entering the patch. The coefficients (*D* and *I*) influenced the intensity

101   of these behaviors and each was free to evolve independently of the others. Immigrant-dependent

102   dispersal only occurred if immigrants were present (i.e. if $M_i > 0$). Fixed intercepts were included

103   to set a lower limit to dispersal via each form of information use at 12%. This intercept allowed

104   dispersal to evolve more rapidly without having an impact on the evolved dispersal rate which

105   was always significantly higher (see SOM, Fig. S8). We assumed haploid genetics and clonal

106   reproduction with mutation in 'genes' for the coefficients (*D* and *I*) that affect each

107   informed-dispersal strategy. These behaviors were then used to determine the probability of

108   dispersal associated with *density* (d_D) and *immigrant* (d_I) information sources using the following

109   function:

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111
$$f(x) = \frac{1}{1 + \exp(-x)}$$
(3)

112

113   where *x* is the influence of each form of information described by equations 1 and 2. This

114   function allowed us to convert the biologically meaningful relationships described in equations 1

115   and 2 to probabilities of dispersal d_D and d_I respectively.

116   Because immigrant-dependent dispersal can only occur if immigrants exist (i.e. some

117   dispersal already occurs), we also included a fixed parameter for baseline *uninformed* dispersal

118   (d_U = 0.1) that always occurred prior to the use of either density or immigrant information

119   sources. Dispersers were randomly assigned to a new patch. Dispersers were subsequently

120   counted as immigrants that could influence the behavior of other juveniles during a given

121   dispersal episode in models including immigrant-dependent dispersal. Individual juveniles were

122   selected at random across the metapopulation to take their dispersal decisions. Indeed, those

123   chosen early were much less likely to have seen immigrants than those chosen to make their

124   dispersal decision later.

125   We constructed alternative models of information use to examine the independent effects

126   of density (D-only) and immigrants (I-only) on dispersal as well as their joint co-evolutionary

127   dynamics when individuals could use both forms of information simultaneously (D&I). In

128   models including both density- and immigrant-dependent information (D&I), *all* individuals

129   were capable of using both sources of information and the sum of the two sources of information

130   determined the dispersal probability. This assumption matches empirical findings that individuals

131   use multiple sources of information in decision making (Le Galliard, Ferriere & Clobert 2003;

132   Cote & Clobert 2007b; Cote, Boudsocq & Clobert 2008; Clobert et al. 2009). In the case of

133   simultaneous models, if $d_D + d_I > 1$, then the individual dispersed, otherwise it dispersed with

134   probability $(d_D + d_I)$. The information source used to calculate 'realized' informed dispersal rates

135   in this case was determined by a random draw using the relative dispersal probability of each

136   information source (d_D or d_I).

137   We determined the probability that informed dispersal evolved and the dispersal rate

138   associated with information use using Monte Carlo simulations of 100 trajectories over 1.5×10^6

139   time steps for each set of parameters and each model case. Because all individuals were capable

140   of information use from one or two sources, then all values of the evolved coefficient potentially

141   existed in the population unless the entire metapopulation went extinct. Therefore, we

142   determined that 'evolution' of an informed dispersal strategy had occurred if the evolved

143   coefficient was greater than 0 more often than by chance across simulations since drift should

144   lead to negative coefficients as often as positive ones. This approach gives similar results to

145   quantify evolution if it increases above an estimate of random drift as presented in the

146   supplemental materials (see SOM).

147   Our initial model exploration focused on the use of density and immigrant sources of

148 information and the coevolution of both forms when together. Subsequent models (see SOM)

149 explored the effects of variation in the costs of dispersal, life history, carrying capacity, patch

150 number, environmental stochasticity, variation in baseline dispersal (d_U), the order in which

151 different sources of information are used, and the immigrant information use strategy function.

152

153   **RESULTS**

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155   **Evolution of Information Use: single source of information**

156   We found that informed dispersal could evolve and drive dispersal behavior and

157 metapopulation dynamics under a broad range of contexts. Consistent with other models (Travis

158 et al. 1999; Ronce 2007), we found that density dependent dispersal evolves when it is the only

159 source of information (Fig. 2a, 3). Here we show that the arrival of immigrants also provides

160 useful information that can drive dispersal behavior (Fig. 2b, 3). Indeed, information-dependent

161 dispersal coefficients (D and I) were significantly biased towards positive values in contrast to

162 expectations from drift which should lead to an equal probability of positive and negative values

163 (Sign test: D-only: 97/100 positive trials, P<0.0001; I-only: 99/100 positive trials, P<0.0001).

164 Both density and immigrant dependent dispersal evolved even when in competition with

165 uninformed dispersal (fixed d_U = 10% and when U was allowed to evolve; see SOM and Fig. S9,

166 S10a) and lead to increased dispersal (Fig. 2a,b) despite a highly stable and homogenous

167 landscape. Dispersal reaction norms due to information use illustrate this nicely: local density

168 and immigrant number influence dispersal (Fig. 4a and b respectively) at equilibrium compared

169 to a flat, fixed dispersal rate of uninformed dispersal. Density-dependent dispersal shows a

170   steady increase in dispersal as local density rises (Fig. 4a). In contrast, immigrant-dependent

171   dispersal shows a rapid increase in dispersal with the first few immigrants and then quickly

172   asymptotes at high levels of dispersal (Fig. 4b).

173   For informed dispersal to evolve there must be some benefit to these strategies.

174   Individuals benefit from dispersal when they find a new population with a lower density given

175   that fitness is density-dependent. We compared the density of the new destination patch and an

176   individual's original patch right before reproduction to estimate the benefit of dispersal to that

177   individual. Informed dispersal led to discovery of a less dense patch than the population of origin

178   on average. Both density and immigrant information seemed to present very similar advantages

179   early in the evolutionary process (Fig. S5a,b and Fig. 5a). However, the benefit of informed

180   dispersal was extremely slight (0.5-0.02%) since the landscape was largely homogenous and

181   most populations were very close to their carrying capacity at all times. Environmental

182   stochasticity augmented spatial heterogeneity in patch density and led to a larger benefit during

183   the evolution of informed dispersal (Fig. 5a; Fig. S5; see also McPeek & Holt 1992; Travis &

184   Dytham 1999).

185

186   **Evolution of Information Use: multiple sources of information**

187   Coexistence of density and immigrant dependent dispersal occurred often in our model

188   when both forms of information use were possible (48% of simulations for model D&I; Fig. 2c

189   and 3). Information-dependent dispersal coefficients for both behaviors (D and I) were again

190   significantly biased towards positive values overall in contrast to expectations from drift (Sign

191   test for D&I model: D: 65/100 positive trials, P=0.035; I: 82/100 positive trials, P<0.0001).

192   Reaction norms of density- and immigrant-dependent dispersal both show increases with density

193   or immigrant number respectively and rise well above background levels of uninformed dispersal

194   (Fig. 4c,d). If we contrast these reaction norms to the reaction norms that evolve when only one

195   form of information use is possible, we see that the slope of density dependent dispersal

196   decreases considerably (Fig. 4a vs. c) whereas the shape of the immigrant-dependent dispersal

197   curve changes only slightly (Fig. 4b vs. d; dispersal above 98% at 3 vs. 5 immigrants

198   respectively). Optimal levels of density-dependent dispersal therefore shift considerably when

199   another source of information affects dispersal. In contrast, immigrant-dependent information

200   has large effects on dispersal with the arrival of the first few immigrants and this trigger does not

201   change much when other sources of information are available.

202   While both forms of dispersal evolved less often when both were present (a decrease of

203   32% and 17% for density and immigrant dependent dispersal respectively), coexistence remained

204   high when in competition with a second source of information (D&I) relative to models where

205   just one strategy was possible (D-only or I-only; Fig. 3). Joint evolution of both information use

206   behaviors occurred even in competition with uninformed baseline dispersal (see SOM, Fig. S9,

207   S10, S11).

208   Informed dispersal showed benefits at the metapopulation level when both forms of

209   information were used together relative to using just one source of information. This benefit was

210   most apparent when demographic stochasticity increased. Lower population carrying capacities

211   raised the risk of extinction due to increased demographic stochasticity, and for a narrow window

212   of carrying capacities the use of two sources of information helped reduce the risk of extinction

213   for the metapopulation as a whole by 20-40% relative to use of just one source of information

214   (Fig. 5d). At slightly lower carrying capacities, when metapopulation extinction always occurred,

215   the use of two different sources of information lead to longer persistence (200-10000 time steps

216   or roughly 100-5000 generations; Fig. S3) of the metapopulation than if just one source of

217   information was used. An increase in the frequency of environmental stochasticity lead to higher

218   metapopulation extinction, and the risk of extinction was lower when one or more sources of

219   information was available (D-only or I-only or D&I) compared to uninformed dispersal only

220   (U-only) (Fig. 5c).

221

222   **DISCUSSION AND SYNTHESIS**

223

224   Our results show that informed dispersal evolves under a broad array of contexts and that

225   both density and indirect immigrant-dependent information sources evolve and can coexist. The

226   frequent evolution of informed dispersal in the very conservative setup examined here (e.g.

227   stable metapopulation) suggests that use of a variety of information sources, including indirect

228   measures of the metapopulation landscape, could be common in nature. Indeed, direct

229   information use in dispersal decisions is widespread (Ims & Hjermann 2001; Matthysen 2005;

230   Ronce 2007; Clobert et al. 2009; Schmidt et al. 2010) and the few empirical investigations of

231   indirect information use that we are aware of have found evidence for it despite a broad

232   taxonomic range. For example, common lizards modify their dispersal behavior in response to

233   immigrants who appear to provide information about the density of their natal population (Cote

234   & Clobert 2007a). Likewise, our recent work in *Tetrahymena* ciliates shows that residents alter

235   their dispersal rate when arriving immigrants come from populations that differ in density or

236   social structure. In both of these empirical examples, immigrants carry more information (e.g.

237   population density) than we included in our model. This additional information should serve to

238   increase the fitness benefits of immigrant-dependent dispersal suggesting that we have probably

239   underestimated the likelihood that it evolves.

240   For use of both information sources to evolve, there must be benefits to adjust behavior

241   using two sources of information rather than a single source. Benefits of density-dependent

242   dispersal are well known since movement out of high density patches should have direct fitness

243   benefits when reproduction is density dependent (Travis et al. 1999). Our results demonstrate

244   that even under very conservative conditions, immigrant dependent dispersal also presents a

245   benefit and evolves. Likewise, coexistence of density- and immigrant-dependent dispersal under

246   the stable meta-population structure that we modeled suggests that these behaviors can evolve

247   and coexist frequently even when the benefits of each behavior are low. Coexistence also implies

248   that neither source of information carries benefits that would cause competitive exclusion of the

249   other information source. Using two sources of information also provided additional benefits and

250   could play an important role in metapopulation stability, especially as increased stochasticity

251   creates larger inequalities in population densities. While the benefits we measured in our model

252   were small in the relatively homogenous landscape we constructed, conditions that more

253   realistically imitate empirical landscapes should confer much larger benefits to this behavior.

254   Joint evolution of density and immigrant dependent dispersal would be prevented if

255   information content of density and immigrant number were not sufficiently different or if one

256   information source was superior to the other (Enfjäll & Leimar 2009; Hovestadt et al. 2010;

257   Schmidt et al. 2010; Bocedi et al. 2012). Immigrant arrival might be related to the overall density

258   of the metapopulation since populations that have more individuals will generate more

259   dispersers, and therefore immigrants, even through a fixed baseline dispersal rate. This estimate

260   of the overall metapopulation density contrasts to density-dependent measures of the local

261 population alone. Competitive exclusion might be expected since immigrant number should be

262 more decoupled with local fitness in any single patch and thus dispersal should carry a higher

263 variance in benefits relative to direct information on local density. Yet we frequently found

264 coexistence of information use through both density and immigrant information. This suggests

265 that each source of information is not fully redundant and that one source of information is not

266 necessarily superior to the other. This equivalency of information can serve as an advantage

267 under some contexts (e.g. when stochasticity is high; Fig. 5 and S3) and would be especially

268 useful where the costs of information use from one source might constrain dispersal below an

269 optimal level (Bocedi et al. 2012). Likewise, if immigrants also carry additional information

270 about their populations (Cote & Clobert 2007a) or help orient dispersers towards certain

271 populations, then we could expect the benefits of indirect information use to be even more

272 advantageous.

273 The potential prevalence of informed dispersal has a number of important implications

274 for both fundamental and applied ecology. In basic ecological research, the use of information

275 has recently been explored in terms of density dependent dispersal, and this simple behavior

276 greatly effects how movement influences population persistence (Ims & Hjermann 2001; Cadet

277 et al. 2003; Matthysen 2005). Earlier models of 'informed' dispersal—such as 'ideal free

278 distribution models—generally assumed perfect knowledge of the landscape (Abrahams 1986;

279 Gray & Kennedy 1994; Holt & Barfield 2001) which presumably was acquired through

280 prospecting that carried low costs. Low cost prospecting might work when patches are close (e.g.

281 foraging patches), but is less realistic when habitat patches are more distant. The use of indirect

282 information, such as the arrival of immigrants, could provide another mechanism by which the

283 ideal free distribution is achieved (Baguette, Clobert & Schtickzelle 2010). If immigrant arrival

284   is linked to overall metapopulation density and if immigrants carry additional information about

285   the quality of those habitats as suggested in empirical examples (Cote & Clobert 2007a), then we

286   might approach an ideal free distribution through use of indirect information transfer across the

287   landscape. Deviation from ideal free models might then in part reflect the quality or reliability of

288   that indirect information transfer (see also Abrahams 1986; Gray & Kennedy 1994; Chaine &

289   Clobert 2012). Most likely, individuals use a number of sources of information on local

290   conditions, direct prospecting of nearby patches, and indirect measures of the landscape such as

291   immigrant-borne information (Clobert et al. 2009). If this form of information use is prevalent,

292   then we must shift our view of dispersal from largely random movement among populations to

293   much more targeted and informed movement patterns that approach ideal-free expectations.

294   Connectivity and dispersal are crucial aspects of population persistence, yet studies of

295   dispersal and metapopulation dynamics usually ignore the important role that information

296   transfer across the landscape might play in guiding subsequent dispersal decisions. Applied

297   management or conservation efforts to increase connectivity or gene flow might be greatly

298   hampered if we do not also introduce the indirect cues that influence dispersal. Indeed, the highly

299   variable success of artificial corridors (Gilbert-Norton et al. 2010) could in part be caused by the

300   lack of indirect information since immigrants will be rare when a new corridor is first

301   constructed (see also Le Galliard et al. 2003). More generally, conservation efforts could be

302   greatly aided by modifying natural dispersal through the manipulation of information that is

303   accessible to residents rather than by costly alterations of the landscape between habitat patches

304   (Chaine & Clobert 2012). As we show here, access to multiple sources of information may better

305   mitigate extinction risk in highly stochastic environments compared to situations where little

306   information exists. Broader inclusion of how information is used in dispersal should provide us

307 with new tools for conservation and fundamentally modify our approach to conservation ecology

308 and the management of populations in peril.

309   Our findings also have important implications for dispersal theory and the incorporation

310 of information use into this field. We found the evolution of both forms of informed dispersal

311 despite potentially large differences in the quality of information gleaned from each source.

312 Whereas local density directly affects fitness, immigrant arrival at best gives some indication of

313 surrounding population sizes when density dependent dispersal exists and at worst simply

314 provides evidence that other populations exist. Coexistence of the two sources of information

315 suggests that the quality of information may be somewhat less important than the presence of

316 that information. In support of this notion, models of indirect information use based on

317 immigrant presence rather than immigrant number show very similar results (Fig. S12). This

318 result is empirically supported by the fact that dispersal in the common lizard was found to be

319 sensitive to the presence and not to the quantity of immigrants (Cote & Clobert 2007a).

320 Similarly, recent models of density dependent information use suggest that the precision of

321 information provides diminishing returns and high quality information is not optimal when it

322 also incurs elevated costs associated with gathering additional precision (Bocedi et al. 2012).

323 Both of these investigations adopt very simple dispersal contexts and yet both show that

324 information use in dispersal evolves quite readily and should be common in nature. More

325 generally, the passive information transfer across the landscape that evolves in our models could

326 be an important first evolutionary step that allows more active information transfer and

327 communication to evolve both within populations and across landscapes.

328

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330

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332

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Figure 1

Life cycle of organisms in the model

Diagram of the basic life cycle of individuals in the model. The two age classes of reproductive individuals are described by their age-specific survival (s) and fecundity (f).

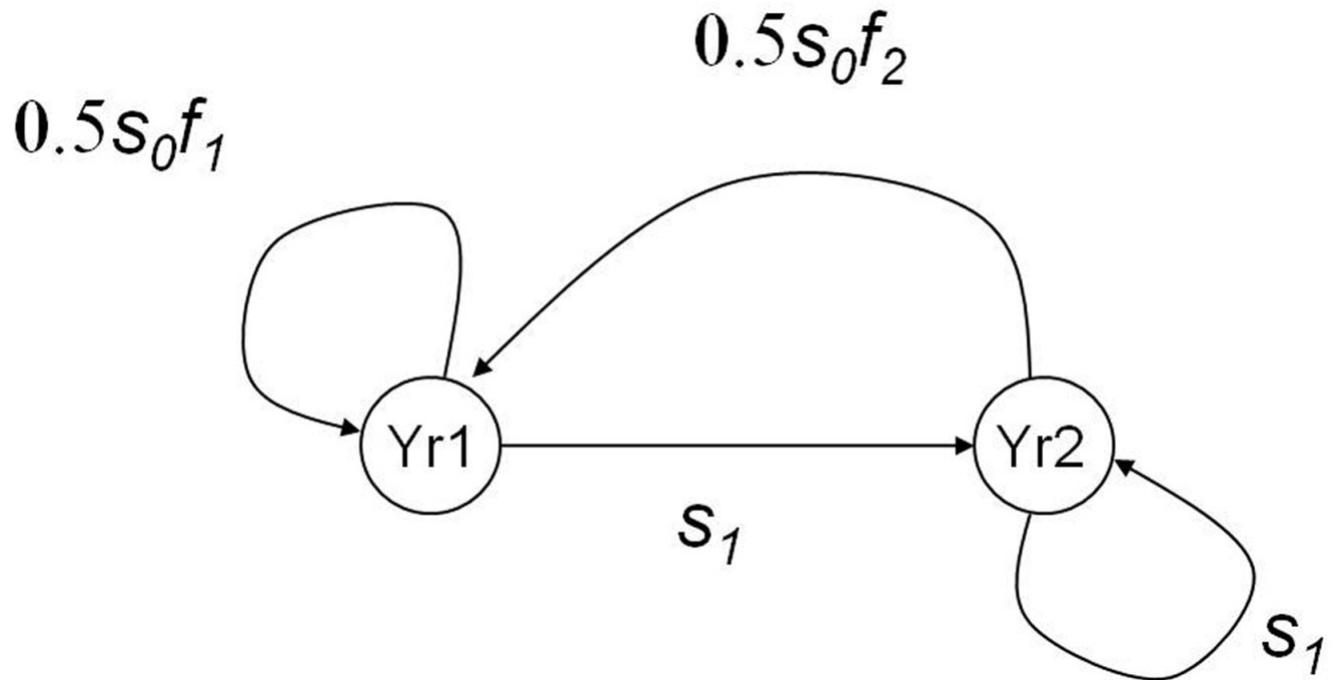



Figure 2

Temporal dynamics of the evolution of informed dispersal

Temporal dynamics of the evolution of information based dispersal due to local density (d_D in red) and the number of arriving immigrants (d_I in blue). Trajectories reflect average dispersal rates for 100 Monte Carlo simulations. A) Dynamics of immigrant number information use alone (d_I). B) Dynamics of density dependent information use alone (d_D). C) Dynamics of both density dependent and immigrant dependent information when used simultaneously (D&I) with no cost of dispersal and D) when density dependent information use reduce survival to 0.99. Uninformed dispersal is fixed at 10% and does not evolve. The 95% confidence interval is shown for the last time step on each trajectory.

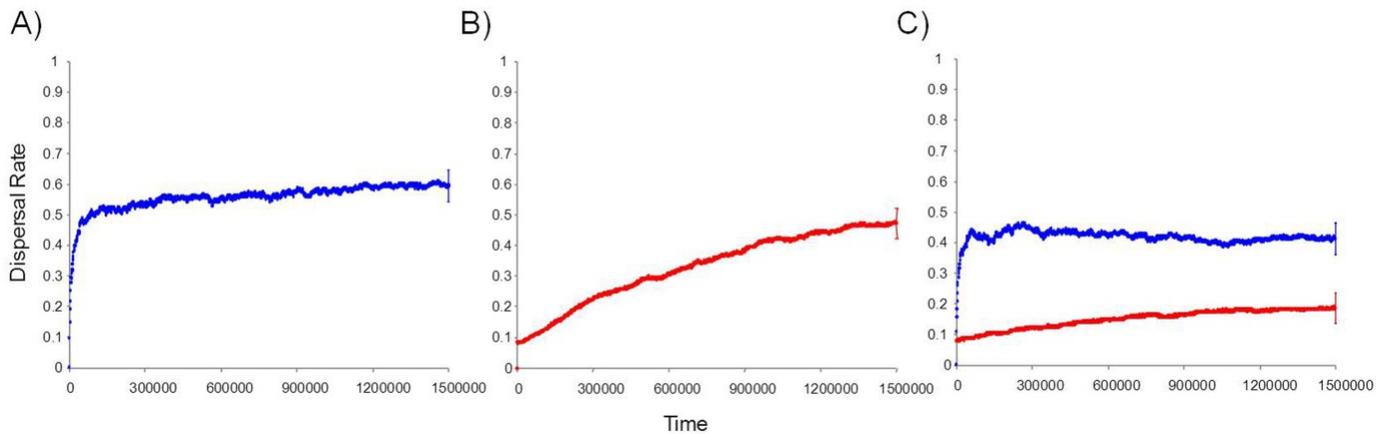



Figure 3

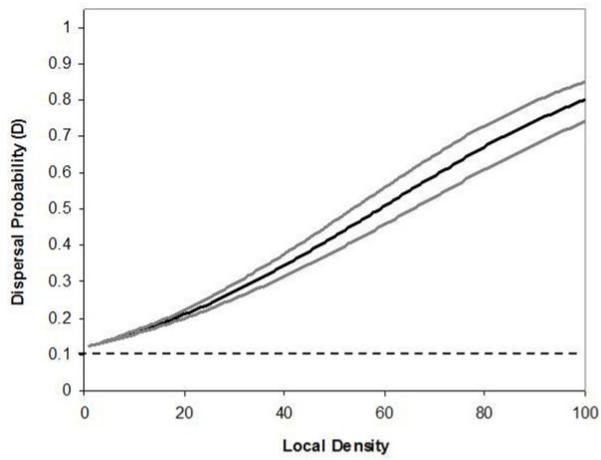
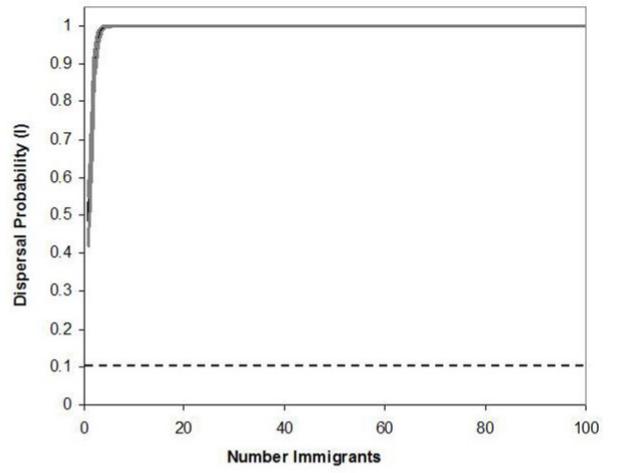
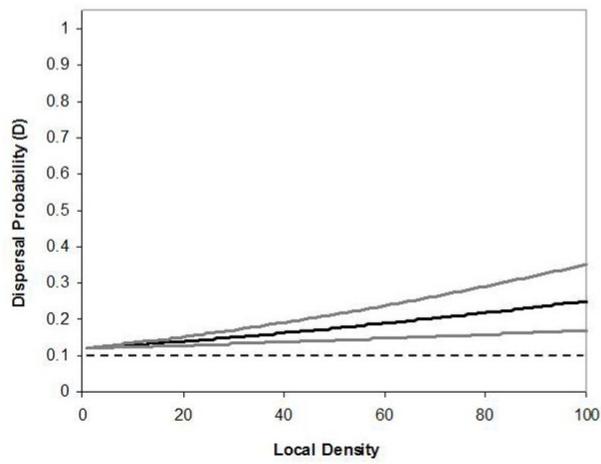
Evolution of information use

Probability that each form of information use evolves. Plotted are the proportion of simulations where dispersal evolved based on density dependent information (D, red), immigrant information (I, blue), both density and immigrant information (D+I, red and blue hatch), or where dispersal did not evolve (None, white) across 100 Monte Carlo simulations. D-alone and I-alone are for models with just one source of information available (plus U fixed at 10%). D&I is a model with both density and immigrant dependent dispersal present. Probability that each form of information use evolves. Plotted are the proportion of simulations where dispersal evolved based on density dependent information (D, red), immigrant information (I, blue), both density and immigrant information (D+I, red and blue hatch), or where dispersal did not evolve (None, white) across 100 Monte Carlo simulations. D-alone and I-alone are for models with just one source of information available (plus U fixed at 10%). D&I is a model with both density and immigrant dependent dispersal present. Probability that each form of information use evolves. Plotted are the proportion of simulations where dispersal evolved based on density dependent information (D, red), immigrant information (I, blue), both density and immigrant information (D+I, red and blue hatch), or where dispersal did not evolve (None, white) across 100 Monte Carlo simulations. D-alone and I-alone are for models with just one source of information available (plus U fixed at 10%). D&I is a model with both density and immigrant dependent dispersal present.

Figure 4

Behavioral reaction norms of informed dispersal

Reaction Norms for informed dispersal behavior. Solid lines show the reaction norms (black) and 95% CL (grey) for each form of dispersal. Dashed lines reflect uninformed baseline dispersal. Reaction norms were created using the Informed Dispersal equations with the mean evolved coefficient after 100000 generations. Lines for the 95% CL were constructed using the variance in evolved coefficients among 100 Monte Carlo runs. Top panels are for models where only one source of information is possible and show dispersal due to A) density dependent dispersal (D-only) and B) immigrant dependent dispersal (I-only). Bottom panels are for models where only both sources of information are possible (D&I) and show dispersal due to C) density dependent dispersal and D) immigrant dependent dispersal.

A) Density for D-alone

B) Immigrant for I-alone

C) Density for D&I

C) Immigrant for D&I

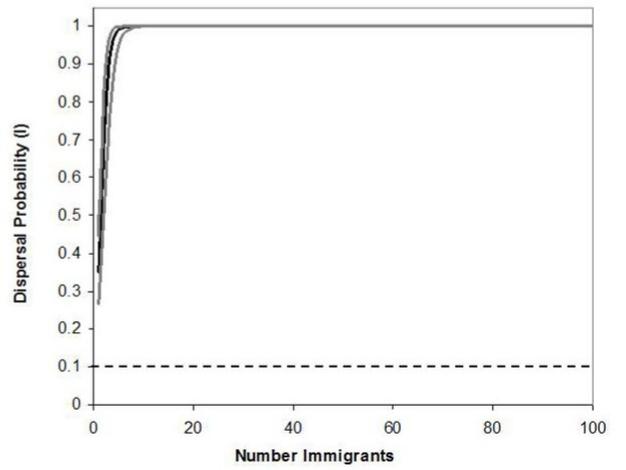



Figure 5

Benefits of informed dispersal

The relative benefit of dispersal behavior to an individual is estimated by how much better a disperser did by moving (i.e. old pop density/ new pop density, both at reproduction). Shown is the dispersal benefit over the first 100000 time steps for models with low environmental stochasticity (5% of populations hit) in models A) I-only (D-only is similar) or B) D&I. Benefits of multiply-informed dispersal (D&I) relative to using no information or a single source of information (D or I-only) is also observed at the meta-population level by reducing global extinction risk (proportion of 100 Monte Carlo simulations where the metapopulation goes extinct) as stochasticity increases due to C) random environmental stochasticity or D) small population size.