

Title: Should dispersers be fast learners? Modelling the role of cognition in dispersal syndromes

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21 **Abstract**

22

23 Both cognitive abilities and dispersal tendencies can vary strongly between individuals. Since
24 cognitive abilities may help dealing with unknown circumstances it is conceivable that
25 dispersers may rely more heavily on learning abilities than residents. However, cognitive
26 abilities are costly and leaving a familiar place might result in losing the advantage of having
27 learned to deal with local conditions. Thus, individuals which invested in learning to cope
28 with local conditions may be more reluctant to leave their natal place. In order to
29 disentangle the complex relationship between dispersal and learning abilities we
30 implemented individual-based simulations. By allowing for developmental plasticity,
31 individuals could either develop a 'resident' or 'dispersal' cognitive phenotype.
32 In line with our expectations, the correlation between learning abilities and dispersal could
33 take any direction, depending how much time individuals had to recoup their investment in
34 cognition. Both, longevity and the timing of dispersal within lifecycles determine the time
35 individuals have to recoup that investment and thus crucially influence this correlation. We
36 therefore suggest that species' life-history will strongly impact the expected cognitive
37 abilities of dispersers, relative to their resident conspecifics, and that cognitive abilities
38 might be an integral part of dispersal syndromes.

39

40 **Keywords**

41 Cognitive styles, behaviour syndromes, life-history, cognition, invasion, pace-of-life

42

43

44 Introduction

45

46 Individuals of the same species differ in their cognitive abilities (Boogert et al. 2018;
47 Cauchoix M. et al. 2018; Liedtke and Fromhage 2019a) and behaviour (e.g. personalities
48 (Kralj-Fišer and Schuett 2014; Réale et al. 2007; Sih et al. 2004)), including dispersal.
49 Regarding the latter, there is accumulating evidence that dispersing individuals are often a
50 non-random subset of their source population. For example, under intraspecific competition
51 it is assumed that weaker individuals are driven out and thus more likely to disperse (D.
52 Bonte and de la Pena 2009). However, under the perspective of inclusive fitness, it has been
53 suggested that kin competition can lead to stronger and more competitive individuals
54 leaving their natal place and compete with non-kin in new patches (D. Bonte and de la Pena
55 2009; Gyllenberg et al. 2008). Dispersal is a complex process which can be divided in three
56 phases: departure, transfer and settlement (Bowler and Benton 2005). Because all three
57 phases involve challenges different to the day-to-day challenges an individual faces when
58 staying at its natal place, dispersing individuals may adjust their phenotypic traits
59 accordingly. When multiple such traits are shaped in concert this is called a 'dispersal
60 syndrome' (Clobert et al. 2009; Cote and Clobert 2012; Legrand et al. 2016). Such 'super
61 dispersers' can have different morphological features to facilitate movement (e.g wing- or
62 body-size; reviewed in Dries Bonte et al. 2012), or may be expected to have different
63 behavioural responses e.g. towards predators (compare Geffroy et al. 2020), or unknown
64 objects (compare Mettke-Hofmann et al. 2005).

65

66 While cognitive abilities may be beneficial during all three dispersal stages (Clobert et al.
67 2009; Cote and Clobert 2012; Delgado M. M. et al. 2014; Edelaar et al. 2017; Maspons et al.

2019; McNamara and Dall 2011), there is not much known about how individual differences in cognitive abilities may relate to differences in dispersal tendencies. Furthermore, cognitive abilities, in general, are expensive and when dispersers settle in an environment in which these abilities are less needed, the costs may outweigh their benefits. Thus, under some circumstances it may be better for dispersers to have lower cognitive abilities in order to save these costs. It is therefore conceivable that cognitive abilities can be developmentally adjusted for dispersal, thus being an integral part of ‘dispersal syndromes’.

In another study we showed that dispersal tendency and learning abilities can evolve in a correlated manner in a metapopulation setting (Liedtke and Fromhage 2021), where distinct trait combinations emerged across different habitat (patch) types. That study, however, made the simplifying assumption that an individual’s learning abilities were fully determined by its genotype, regardless of whether it dispersed or not. This essentially meant that different traits could not influence each other during development, thus precluding the evolution of an optionally expressed ‘dispersal syndrome’ involving multiple traits. The present study is designed to relax this constraint. To this end, we model the evolution of a genotypic strategy that can encode two independently evolving alternative phenotypes – a ‘resident’ and a ‘disperser’ phenotype which are expressed in these respective contexts. Specifically, we assume that each individual faces a developmental switch with two options: either it expresses its genotypically encoded ‘resident’ phenotype and is then destined not to disperse; or it expresses its genotypically encoded ‘disperser’ phenotype and is then destined to disperse. This modelling approach seems especially appropriate for species where residents and dispersers differ in traits linked to dispersal, even among individuals originating from the same patch. Wing-dimorphism, for example, is commonly found in

insects, with large-winged (macropterous) individuals constituting the dispersal morph (Roff 1986), which also may be linked to metabolism specialisation (Van Belleghem and Hendrickx 2014). Furthermore, whether the investment in cognitive abilities can be recouped, and thus can be adaptive, crucially depends on how much time animals have available to use these abilities (Liedtke and Fromhage 2019b and ref. therein). We therefore investigate the effects of longevity and timing of dispersal on the interplay between cognitive abilities and dispersal, as both aspects crucially determine the duration of this recouping phase. This allows us to assess the role of life-history traits in shaping dispersal syndromes.

Methods

This model is an extension of a previous (Liedtke and Fromhage 2021) model about the joint evolution of cognitive styles and dispersal tendencies. The description of methods is therefore largely identical, except for the implementation of developmental plasticity (see below) and the exclusion of predation (for simplicity).

We implemented a metapopulation setting with N_{patches} habitat patches, which are connected through random global dispersal, i.e. individuals have the same chance of reaching any of the N_{patches} patches when dispersing (list of abbreviations see Table 1). Carrying capacity of each patch is set to $N_{\text{individuals}}$ and three traits are allowed to evolve independently for $N_{\text{generations}}$: learning ability L , exploration tendency E , and dispersal tendency D . All three traits are continuous with values between 0 and 1. At the end of each generation, individuals reproduce asexually in proportion to their fitness. Fitness of individuals is specified by the amount of resources they obtain during their lifetime. We assume an ‘income breeder’

116 system where individuals may reproduce independently of their survival until the end of
117 season.

118 The length of a season (= generation) is defined by the number of days before dispersal
119 T_{before} , plus the number of days after dispersal T_{after} . For simplicity, dispersal does not
120 consume any time. Cost of dispersal is implemented as mortality risk M during dispersal.

121 The lifecycle of individuals proceeds in four phases: 1) time before dispersal in which they
122 can collect resources; 2) potential dispersal event i.e. moving with some probability from
123 one patch to another, with a mortality risk defined by M ; 3) time after dispersal for collecting
124 resources; 4) asexual reproduction followed by death. After the last phase a new generation
125 starts with offspring generated by the parent generation.

126

127 Development

128 Because optimal traits values (L and E) may differ for residents and dispersers, we allow for
129 developmental plasticity, by letting the expression of L and E to be conditional on dispersal.

130 We implement two loci for learning abilities: one locus determines the L value for residents
131 (L_R) and the other for dispersers (L_D). Similarly, there are two loci for exploration tendency

132 with E_R encoding exploration for residents and E_D for dispersers. Traits do not change at the
133 time of dispersal, but instead remain constant throughout an individual's life. Whether or

134 not an individual will disperse is determined at the beginning of its life, depending on its trait
135 value D and a threshold value between 0 and 1 randomly drawn from a uniform distribution.

136 When the individual's dispersal tendency (D) is higher than that threshold the individual will
137 disperse; otherwise it will stay at its natal place. If the individual will be a resident, it

138 expresses L_R and E_R ; if it will disperse, it expresses L_D and E_D , respectively. Each locus

139 underwent independent mutation as described below and thus could evolve independently.

140

141 Environment

142 The environment of a patch is defined by its patch size $N_{Individuals}$ and the abundance (A_{Ri}) of
143 different resource types R_i . Abundances are defined as the maximal number of resource
144 items of type R_i which an individual can encounter in a given period of time (see below).
145 Furthermore, resources are defined by their value V_{Ri} in terms of increasing fitness, their
146 handling time H_{Ri} i.e. how long individuals need to handle them before they can obtain their
147 value, and their detectability C_{Ri} , i.e. how easy they are to find.

148

149 Learning

150 Learning is implemented as a reduction in handling-time (H_{Ri}) of resources due to gaining
151 experience with specific resource types, reflecting the idea that some feeding techniques
152 need to be practiced repeatedly before succeeding (such as tool use in primates (Boesch et
153 al. 2019) and birds (Kenward et al. 2006), or hunting techniques in dolphins (Guinet and
154 Bouvier 1995)). Up to ten different resource types are implemented, with R_1 being a simple-
155 to-access resource whose handling requires no learning. R_2 to R_{10} are resources for which
156 individuals need experience before they can exploit them. Therefore, individuals get better
157 at exploiting resource items of type R_2 through R_{10} with time. Learning experience with
158 specific resource types can be carried over to new settlement patches if dispersers will find
159 the same resource type in the new patch. A detailed description of how learning was
160 calculated follows below.

161

162 Resource intake

163 First, we calculate the maximum number of resource items per type (R_i) an individual can
 164 collect before dispersal, by multiplying the abundances (A_{Ri}) in patch P_i with the time it has to
 165 do so (i.e. T_{before}). Based on the results found in a previous study (Liedtke and Fromhage
 166 2019a), we assumed that individuals will at least move every second time step. Whether
 167 individuals would also move in the other timesteps depends on their exploration tendency
 168 (E_i). The higher its E_i the more likely an individual moves and encounters further resources,
 169 such that its maximum number of resource items of type R_i is given by

170

$$171 \quad N_{Ri} = A_{Ri} * T_{before} * (1 + E_i) \quad 1.$$

172

173 This formulation implies that individuals with $E_i = 0$ move with a slow pace and gain
 174 maximally half of what individuals with $E_i = 1$ gain.

175

176 Next, we take into account the individuals' exploration tendency E_i and the detectability of
 177 resource types C_{Ri} . We assume that the faster an individual explores, the less thoroughly it
 178 can search; and the harder the items are to detect (i.e. low C_{Ri}), the less likely the individual
 179 will find a resource. This changes the calculation of collected resources as:

180

$$181 \quad N_{Ri}' = N_{Ri} * (1 - (1 - C_{Ri}) * E_i) \quad 2.$$

182

183 Thereafter, we take into account each individual's efficiency of handling resources as
 184 influenced by its learning speed L and the number of resource items collected, i.e. how much
 185 experience it gained with a specific resource type. This changes the calculation of collected
 186 resources as:

187

$$188 \quad N_{Ri}'' = \sum_{j=1}^{\text{round}(N_{Ri}')} \max\left(0, 1 - \frac{\sqrt{H_{Ri}} - 1}{\sqrt{j * L}}\right) \quad 3.$$

189

190 where H_{Ri} is the handling-time of R_i . This formula was selected because it describes a decline
 191 of handling time at a decelerating rate. This functional shape appears biologically plausible
 192 because perfection may often be difficult to reach, which may slow progress down once
 193 more progress has been made. Note that resources with high H need to be handled multiple
 194 times before they can be exploited by a given individual.

195

196 Finally, we take into account intraspecific competition over resources within a patch. First
 197 we estimate the maximum total amount of resources $Rmax_i$ potentially collected by all
 198 individuals in a given patch, adjusted by a competition factor Φ that controls the severity of
 199 the competition:

200

$$201 \quad Rmax_i = T_{before} * A_{Ri} * N_{individual} / \Phi \quad 4.$$

202

203 Then we divide this by the sum of resources collected by all individuals as estimated by eq. 3,
 204 to obtain the ratio $Rmax_i / \sum N_{Ri}''$. If this ratio is < 1 , then the focal resource type is completely
 205 depleted, and the share collected per individual is reduced by competition as:

206

$$207 \quad N_{Ri}''' = N_{Ri}'' * Rmax_i / \sum N_{Ri}'' \quad 5.$$

208

209 For example, if (according to pre-competition calculations) resource type R_2 was collected 10
 210 times more often than its R_{max_i} value for this patch, then for every individual in this patch its
 211 amount of collected R_2 items is multiplied by 0.1.

212

213 Dispersal

214 After this foraging phase, individuals could disperse to a randomly chosen patch. An
 215 individual's decision to disperse or not was determined at the beginning of its life as
 216 described above. Due to the stochasticity of this process some patches may have lower,
 217 other patches higher numbers of individuals after the dispersal phase. Dispersal costs are
 218 implemented as mortality risk M which was set to 0.01 in all cases. Whenever an individual
 219 attempts to disperse, a random number between 0 and 1 is drawn from an uniform
 220 distribution. If this number is lower than M , the individual dies; otherwise it successfully
 221 disperses.

222

223 After the dispersal phase, surviving individuals are allowed to collect resources again.
 224 Resource intake and competition are calculated as in the pre-dispersal phase (eqns. 1 – 5)
 225 with the only difference being that the duration of the post-dispersal phase is defined by

226 T_{after} .

227

228 Reproduction

229 After estimating the total resource income of all individuals, reproductive success (fecundity)
 230 is calculated as:

231

$$232 \quad F = V_{Total} * (1 - L * \alpha) \quad 8,$$

17 10

18

233

234 where L is an individual's learning ability, α a cost coefficient which specifies the cost of
235 learning, and V_{Total} is the sum of value of all resources collected by this individual. We do not
236 include any explicit cost of E because costs of exploration are implicit in the risks of
237 overlooking resources. The next generation is recruited in each patch independently, by
238 using F of local individuals as the independent sampling probability. Thus, the higher F of a
239 focal individual is compared to all other individuals in the same patch, the more likely it
240 contributes offspring to the total $N_{Individuals}$.

241

242 Mutation

243 Mutation probabilities for all three traits (L, E, D) are set to $\mu = 0.1$. Traits evolve
244 independently and new values are chosen randomly from a normal distribution with the
245 parental trait value as mean and SD of 0.1.

246

247 Extinction

248 To increase the incentive to disperse, it is common practice in modelling studies to
249 implement random extinction of patches (Poethke et al. 2003). We do so by erasing, with a
250 given frequency, all individuals of a randomly selected patch in the end of a generation. The
251 empty patch can only be recolonised by emigrants from other patches within the
252 metapopulation.

253

254 Initialisation

Initially we heuristically explored the parameter space in order to find parameter settings allowing the evolution of different cognitive styles which can coexist both within (compare Liedtke and Fromhage 2019a) and between patches.

For simplicity, the main results presented here are derived from simulations in which detectabilities of resources (C_{Ri}) were the same and thus E of all individuals evolved to be similar. This allows us to concentrate on the effects of learning abilities on dispersal and vice versa, which is our main interest here.

Parameter settings for each of the presented simulation sets are given in tables (Table 3, Table 3). All simulations presented were replicated 10 times with identical parameter settings in order to check for consistency. All replicate runs produced qualitatively similar results.

Results

Season length (i.e. T_{before} and T_{after}) crucially determines whether dispersers had higher or lower L than residents (see Figure 1). With very short lifespans individuals did not invest into higher learning speed and both L_R and L_D were low accordingly. However, since dispersal tendency D was very high, there were only very few residents present and thus selection for L_R was low. Due to mutation-selection balance (Crow and Kimura 1970), L_R was pushed upwards (Fig.1, $SL = 4$ and 10), i.e. closer to the value 0.5 expected for a selectively neutral trait. With slightly longer season length, residents, which, by definition, stayed in their birth patch their whole life, became able to exploit hard-to-access resources if they invested

279 strongly into learning abilities (i.e. L_R). This led to a huge increase in L_R compared to learning
 280 abilities of dispersers (i.e. L_D) which were unable to exploit hard-to-access resources within
 281 their given time (Fig. 1, $SL = 20$ and 30). When increasing the total season length further, also
 282 dispersers were able to exploit hard-to-access resources (both in their natal and new
 283 settlement patches) and invested highly into L . As a result, the differences between L_R and L_D
 284 first becomes insignificant (Fig. 1, Tab. 2, $SL=50$) and then, with increased SL , reverses
 285 direction i.e. L_R becomes significantly lower than L_D . (Fig. 1, Tab. 2, $SL > 50$).
 286 Changing the timing of dispersal within the life cycle strongly influenced the cognitive style
 287 of disperses. When dispersal took place in the middle of life, dispersers invested little in
 288 learning when they didn't have enough time to learn either at their birthplace or at the new
 289 patch. However, when dispersal took place either early or late in life (e.g. breeding
 290 dispersal), then dispersers had time to adapt to at least one set of local conditions, hence
 291 investing in L similarly to residents (see Fig. 2).

292 Discussion

293 Our model revealed strong effects of longevity and the timing of dispersal on evolved
294 patterns in learning abilities. While sufficient longevity was generally needed for the
295 evolution of high learning abilities, the timing of dispersal modulated the relationship
296 between learning abilities and dispersal, which could be either positive or negative.

297

298 Similar to a previous model (Liedtke and Fromhage 2019a), resource composition
299 determines whether or not different cognitive styles can coexist within the same patch. The
300 coexistence depends on individuals specialising on different resource types, such that some
301 individuals specialize on more abundant and easy-to-handle resources, whereas others
302 specialise on hard-to-access resources with higher value. Since individuals compete over
303 these resources, negative frequency-dependence stabilises the coexistence. For the hard-to-
304 access resources, individuals need to invest into learning speed (L) in order to be able to
305 learn to exploit them within the available time (i.e. lifespan). With very short lifespans time
306 is not sufficient for learning and thus no investment in L occurred. Once there is enough time
307 for learning to exploit these resources, any further increase in lifespan leads to a reduced
308 investment in L because of relaxed time pressure (i.e., individuals can reduce learning costs
309 by learning more slowly, provided there is enough time; compare (Liedtke and Fromhage
310 2019b)). This non-linear link between lifespan and investment into learning speed is the
311 underlying cause of the effect of lifespan on dispersal in the present model. With very short
312 lifespans, individuals do not invest in higher L and consequently residents and dispersers
313 adopt similar cognitive styles with low learning abilities (Figure 1, leftmost datapoints). Yet, if
314 lifespan is just long enough for learning to handle hard-to-access resources, individuals need
315 to invest highly in L in order to exploit these resources. Crucially, only if fast-learning

316 individuals encounter these resources throughout their whole life, they can recoup the
317 investment into high L . So, if hard-to-access resources differ between patches, and learning
318 progress is not transferable between resource types, then dispersers are unable to exploit
319 hard-to-access resources either at their natal or at the settlement patch. Therefore,
320 dispersers cannot recoup their investment into high L . Consequently, individuals investing
321 into high L are better off staying in their natal place, and dispersers are better off investing
322 little into L , specialising on easy-to-access resources instead (Figure 1, centre).

323

324 With increased lifespans, the pattern reverses because above a given minimal lifespan, there
325 is sufficient time for learning to handle resources both at the natal place as well as in new
326 environments faced after dispersal. Meanwhile, since residents only need to learn one type
327 of hard-to-access resource they have more time to do so and can afford to learn slower and
328 pay less cost of L . Accordingly, dispersers have higher L than residents (Figure 1, right half).
329 With further increase in lifespan also dispersers have more time to learn and thus can
330 likewise afford to reduce their investment in L .

331

332 A similar effect occurs when considering the timing of dispersal within the lifecycle of a
333 species. Dispersal early in life allows dispersers to adjust to local conditions of the settlement
334 patch where they spend most of their life. Provided that lifespan is not too long (see above)
335 this promotes the investment into L for dispersers, to a similar extent as in residents.
336 Likewise, dispersal at the end of the lifecycle (i.e. breeding dispersal) allows individuals to
337 adjust to local conditions of the natal place where they spend most of their life. Again, this
338 leads to minimal differences in L between residents and locals. If, however, dispersal takes
339 place in the middle of life, it divides the available time in any one place in such a way as to

prevent dispersers from investing in L . Under these circumstances we can find different values of L for residents and dispersers. This relationship, of course, depends greatly on the species' total lifespan. With very short lifespans, no investment in L is expected whereas with very long lifespan, as in long-living vertebrates such as primates or parrots, even dispersal somewhere in the middle of life should allow to adjust both to the natal and the new patch.

Comparing our present results with those of a model without developmental plasticity (Liedtke and Fromhage 2021), we can summarize that under both approaches a correlation between learning abilities and dispersal occurs under a wide range of environmental circumstances. However, the differences between dispersers and residents are clearer when they are based on developmental plasticity. The intuitive explanation for this is that plasticity allows selection to shape alternative specialized phenotypes, for a life that either involves dispersal or not (see e.g. Roff 1986).

Whether such plasticity is to be expected in natural systems depends on the species and, in particular, on the ecological factors that trigger dispersal. As described in the introduction, dispersal is often a conditional process. When triggering conditions occur early in life, such as conspecific density, predation pressure or kin competition, the developmental trajectory of dispersing individuals may be adjusted accordingly. Thus, under these circumstances we suppose that cognitive abilities, like other traits, may differ substantially between residents and dispersers and, in some cases, eventually produce dispersal syndromes. By contrast, when triggering conditions occur after the developmental phase and are not predictable beforehand, for example operational sex-ratio, sudden droughts, flooding, or fire events, individuals are restricted in their adjustment to dispersal. In this case a correlation between

learning abilities and dispersal can arise at the population level through local adaptation, e.g. if some habitat types favour higher values in both learning ability and dispersal tendency (Liedtke and Fromhage 2021). However, according to our simulations, such correlations tend to be less pronounced (and hence may be harder to detect empirically) than under the developmental plasticity scenario.

In conclusion, we have shown that the interplay of cognitive abilities and dispersal can be complex. In our simulations, time is a crucial determinant of whether dispersers should be fast learners in order to adjust quickly to new environments, or whether dispersal interferes with the ability to reap the potential benefits of learning. More generally speaking, plasticity allows individuals to adjust to local conditions which however induces also costs. Whether these costs can be recouped depends on how much time the dispersers have after settlement. We therefore predict that a species' lifespan and the timing of dispersal within the lifecycle crucially influence the correlation between dispersal and cognitive abilities, supporting other findings underlining the importance of lifecycles when considering the evolution of dispersal (e.g. Massol and Débarre 2015). It might be an interesting further avenue of research to investigate whether life-history traits such as lifespan and timing of dispersal coevolve under changing environmental complexity and predictability.

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Data accessibility statement'

388 Code of simulation and data are available at Dryad
389 Dryad DOI: <https://doi.org/10.5061/dryad.76hdr7svb>
390 Dryad review URL:
391 https://datadryad.org/stash/share/2MqxSLfbl94g_BDX1ai8LuTeB8FJk_vUV0m0sVaqtZU

392 **Authors' contributions**

393 JL initiated the project and did the simulations. Both authors, LF and JL, contributed equally
394 to discussion of ideas and writing, have read and approved the manuscript.

395

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488 **Tables**

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490 **Table 1: Abbreviations**

491

ABBREVIATION	DESCRIPTION
A_{RI}	Abundance of different resource types
C_{RI}	Detectability of resource type i
D	Dispersal tendency
E_D	Exploration tendency for dispersers
E_R	Exploration tendency for residents
F	Reproductive success (fecundity)
H_{RI}	Handling-time of resource type i
L_D	Learning ability for dispersers
L_R	Learning ability for residents
M	Mortality risk
$N_{GENERATIONS}$	Number of generations
$N_{INDIVIDUALS}$	Carrying capacity of P_i
$N_{PATCHES}$	Number of patches
N_{RI}	Maximum number of resource items per type per individual
P_i	Patch number i
R_i	Resource type i
$RMAX_i$	Maximum total amount of resources $Rmax_i$ in a given patch
T_{AFTER}	Length of season after dispersal
T_{BEFORE}	Length of season before dispersal
V_{RI}	Value of resource type i
V_{TOTAL}	Sum of value of all resources collected by a given individual
A	Cost coefficient of learning
M	Mutation probability
Φ	Competition factor

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494 **Table 2: Parameter settings for simulation presented in figure 1 main text**
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ABBREVIATION	DESCRIPTION	PARAMETER SETTING
A_{RI}	Abundance of different resource types	In patch type 1: $R_1=1$, $R_2=5$; In patch type 2: $R_1=1$, $R_3=5$
C_{RI}	Detectability of resource type i	$R_1=R_2=R_3=0.5$
H_{RI}	Handling-time of resource type i	$R_1=1$, $R_2=R_3=300$
M	Mortality risk	0.01
$N_{GENERATIONS}$	Number of generations	300
$N_{INDIVIDUALS}$	Carrying capacity of P_i	100
$N_{PATCHES}$	Number of patches	12
T_{AFTER}	Length of season after dispersal	2, 4, 10, 15, 25, 50, 150, 250, 500, 1000, 2000
T_{BEFORE}	Length of season before dispersal	2, 4, 10, 15, 25, 50, 150, 250, 500, 1000, 2000
V_{RI}	Value of resource type i	$R_1=1$, $R_2=R_3=10$
A	Cost coefficient of learning	1.4
M	Mutation probability	0.1
Φ	Competition factor	2
EX_{FREQ}	Extinction frequency (every x generation)	2
EX_N	Number of patches getting erased every EX_{freq} generation	1

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497 **Table 3: Parameter settings for simulation presented in figure 2 main text**
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ABBREVIATION	DESCRIPTION	PARAMETER SETTING
A_{RI}	Abundance of different resource types	In patch type 1: $R_1=1$, $R_2=5$, $R_3=0$ In patch type 2: $R_1=1$, $R_2=0$, $R_3=5$
C_{RI}	Detectability of resource type i	$R_1=R_2=R_3=0.5$
H_{RI}	Handling-time of resource type i	$R_1=1$, $R_2=R_3=150$
M	Mortality risk	0.01
$N_{GENERATIONS}$	Number of generations	500
$N_{INDIVIDUALS}$	Carrying capacity of P_i	100
$N_{PATCHES}$	Number of patches	12
T_{AFTER}	Length of season after dispersal	2, 10, 18
T_{BEFORE}	Length of season before dispersal	18, 10, 2
V_{RI}	Value of resource type i	$R_1=1$, $R_2=10$
A	Cost coefficient of learning	1.4
M	Mutation probability	0.1
Φ	Competition factor	6
EX_{FREQ}	Extinction frequency (every x generation)	2
EX_N	Number of patches getting erased every EX_{freq} generation	1

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