RESEARCH ARTICLE

Should dispersers be fast learners? Modeling the role of cognition in dispersal syndromes

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Abstract

Both cognitive abilities and dispersal tendencies can vary strongly between individuals. Since cognitive abilities may help dealing with unknown circumstances, it is conceivable that dispersers may rely more heavily on learning abilities than residents. However, cognitive abilities are costly and leaving a familiar place might result in losing the advantage of having learned to deal with local conditions. Thus, individuals which invested in learning to cope with local conditions may be better off staying at their natal place. In order to disentangle the complex relationship between dispersal and learning abilities, we implemented individual-based simulations. By allowing for developmental plasticity, individuals could either become a 'resident' or 'dispersal' cognitive phenotype. The model showed that in general residents have higher learning abilities than dispersers. Dispersers evolve higher learning ability than residents when dispersers have long life spans and when dispersal occurs either early or late in life, thereby maximizing the time in one habitat patch. Time is crucial here, because the longer an individual resides in a location where it can use its learned knowledge or behavior, the more often it profits from it and thus eventually obtains a net benefit from its investment into learning. Both, longevity and the timing of dispersal within lifecycles determine the time individuals have to recoup that investment and thus crucially influence this correlation. We therefore suggest that species' life history will strongly impact the expected cognitive abilities of dispersers, relative to their resident conspecifics, and that cognitive abilities might be an integral part of dispersal syndromes.

KEYWORDS
behavior syndromes, cognition, cognitive styles, invasion, life history, pace of life

1 | INTRODUCTION

There is accumulating evidence that dispersing individuals are often a nonrandom subset of their source population. For example, under intraspecific competition it is assumed that weaker individuals are driven out and thus more likely to disperse (Bonte & de la Pena, 2009). However, under the perspective of inclusive fitness, it has been suggested that kin competition can lead to stronger and more competitive individuals leaving their natal place and compete with nonkin in new patches (Bonte & de la Pena, 2009; Gyllenberg et al., 2008).

Dispersal is a complex process which can be divided into three phases: departure, transfer, and settlement (Bowler & Benton, 2005). Because all three phases involve challenges that differ from the day-to-day challenges an individual faces when staying at its natal place, dispersing individuals may adjust their phenotypic traits accordingly. When multiple such traits are shaped in concert, this is called a 'dispersal syndrome' (Clobert et al., 2009; Cote & Clobert, 2012; Legrand et al., 2016; Sih et al., 2004). Such 'super dispersers' can have different morphological features to facilitate movement (e.g., wing or body size; reviewed in Bonte et al., 2012), increased fat reserves (O'Riain et al., 1996), or may be expected to have different behavioral responses to optimize performance in new environments (Sih et al., 2004), for example, toward predators (compare Geffroy et al., 2020), conspecifics (Toor et al., 2020), or unknown objects (compare Mettke-Hofmann et al., 2005).

Species differ quite strongly in their cognitive abilities, which are often positively correlated with longevity (e.g., Deaner et al., 2003; Sol, 2009). However, even short-living species are showing astonishing cognitive abilities, ranging from associative learning in nematodes (Sasakura & Mori, 2013), reversal learning in spiders (Liedtke & Schneider, 2014), to social learning and teaching in insects (Alem et al., 2016). In recent years, it has become clear that individuals of the same species differ in their cognitive abilities (Boogert et al., 2018; Cauchoix et al., 2018; Liedtke & Fromhage, 2019a), raising the question whether these between-individual differences may correlate with other traits such as dispersal, thus potentially being part of a 'dispersal syndrome' as described above.

Cognitive abilities may be beneficial during all three dispersal stages as they allow to, for example, gather information about and to compare unknown habitats (Clobert et al., 2009; Cote & Clobert, 2012; Delgado et al., 2014; Edelaar et al., 2017; Maspons et al., 2019; McNamara & Dall, 2011). Yet, 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 (e.g., metabolic costs, Niven & Laughlin, 2008) 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 adjusted for dispersal during development, 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 & 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. These adjustments are irreversible and cannot be changed during an individuals' lifetime. This modeling 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 specialization (Van Belleghem & Hendrickx, 2014). In naked mole rats, young males can develop into a dispersing morph, including increased fat reserves and behavior adaptations, presumptively for increasing outbreeding (O'Riain et al., 1996). In common lizards, dispersal dimorphism is responsive to environmental change (e.g., fragmentation, Cote et al., 2017). 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 & Fromhage, 2019b and refs. therein). Longevity and timing of dispersal crucially influence the duration of this recouping phase by determining how long an individual will reside in one patch. We therefore investigate the effects of longevity and timing of dispersal on the interplay between cognitive abilities and dispersal. This allows us to assess the role of life-history traits in shaping dispersal syndromes. Because dispersal syndromes have mostly been documented for relatively short-lived species, we note that those are the species for which our present modeling approach may be most likely to be relevant. On the other hand, we see no compelling theoretical reason why the processes studied in our model should not occur, in a qualitatively similar form, in long-lived species too.

2 | METHODS

This model is an extension of a previous model (Liedtke & Fromhage, 2021) 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, that is, 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 (i.e., explorative foraging within patch), 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

TABLE 1 Abbreviations

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 Pi
$N_{Patches}$	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

assume an 'income breeder' system where individuals may reproduce independently of their survival until the end of season.

The length of a season (=generation) is defined by the number of days before dispersal T_{before}, plus the number of days after dispersal T_{after}. For simplicity, all dispersers will disperse at the same moment and dispersal does not consume any time. Cost of dispersal is implemented as mortality risk M during dispersal.

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

2.1 | Development

Because optimal traits values (L and E) may differ for residents and dispersers, we allow for developmental plasticity, by letting the expression of L and E to be conditional on dispersal. Whether or not an individual will disperse is determined at the very beginning of its

life, depending on its trait value D and a threshold value between 0 and 1 randomly drawn from a uniform distribution. When the individual's dispersal tendency (D) is higher than that threshold, the individual will disperse later in life; otherwise, it will stay in its natal place. Depending on the now determined fate of individuals as either a resident or a disperser, they will develop different phenotypes, which are encoded by two independent loci: one locus determines the learning abilities for residents (L_R) and the other for dispersers (L_D). Similarly, there are two loci for exploration tendency with E_R encoding exploration for residents and E_D for dispersers. If the individual will be a resident, it expresses L_R and E_R; if it will disperse, it expresses L_D and E_D, respectively. Traits do not change at the time of dispersal, but instead remain constant throughout an individual's life. Each locus underwent independent mutation as described below and thus could evolve independently.

2.2 | Environment

The environment of a patch is defined by its patch size $N_{Individuals}$ and the abundance (A_{Ri}) of different resource types R_i. Abundances are defined as the maximal number of resource items of type R_i which an individual can encounter in a given period of time (see below). Patches can differ in their composition of available resources. Furthermore, resources are defined by their value V_{Ri} in terms of increasing fitness, their handling time H_{Ri}, that is, how long individuals need to handle them before they can obtain their value, and their detectability C_{Ri}, that is, how easy they are to find. For simplicity, we implemented simulations with two, equally frequent, patch types.

2.3 | Learning

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

2.4 | Resource intake

First, we calculate the maximum number of resource items per type (R_i) an individual can collect before dispersal, by multiplying the abundances (A_{Ri}) in patch P_i with the time it has to do so

(i.e., T_{before}). Based on the results found in a previous study (Liedtke & Fromhage, 2019a), we assumed that individuals will explore their surroundings at least every second time step. Whether individuals would also move in the other timesteps depends on their exploration tendency (E_i). The higher its E_i the more likely an individual moves and encounters further resources, such that its maximum number of resource items of type R_i is given by.

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

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

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

$$N'_{Ri} = N_{Ri} * (1 - (1 - C_{Ri}) * E_i) \tag{2}$$

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

$$N''_{Ri} = \sum_{j=1}^{round(N'_{Ri})} max\left(0, 1 - \frac{\sqrt{H_{Ri}} - 1}{\sqrt{j * L}}\right) \tag{3}$$

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

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

$$Rmax_i = T_{before} * A_{Ri} * N_{Individual} / \Phi \tag{4}$$

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

$$N'''_{Ri} = N''_{Ri} * Rmax / \sum_i N''_{Ri} \tag{5}$$

For example, if (according to precompetition calculations) resource type R_2 was collected 10 times more often than its $Rmax_i$ value for this patch, then for every individual in this patch its amount of collected R_2 items is multiplied by 0.1.

2.5 | Dispersal

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

After the dispersal phase, surviving individuals are allowed to collect resources again. Resource intake and competition are calculated as in the predispersal phase (Equations 1–5) with the only difference being that the duration of the postdispersal phase is defined by T_{after}. Note that dispersers may need to learn how to gain hard-to-access resources again, if a different resource type is found in the settlement patch. Since residents stay in their natal patch, they need to learn only one type of hard-to-access resource type (with given settings presented in this study).

2.6 | Reproduction

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

$$F = V_{Total} * (1 - L * \alpha) \tag{6}$$

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

2.7 | Mutation

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

2.8 | Extinction

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

2.9 | Initialization

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 & 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 2 and 3. All simulations presented were replicated 10 times with identical parameter settings. All replicate runs produced qualitatively similar results.

To compare learning abilities (L) between residents and dispersers, we applied paired t tests. Separately for each season length ($S = 4$ to 4,000), we used the mean values of L of residents and dispersers of each replicated simulation run as independent datapoints (degrees of freedom = 9).

All traits reached equilibrium—as judged by visual inspection—well within given generations numbers.

3 | RESULTS

Season length (i.e., $T_{before} + T_{after}$; equivalent to life span) crucially determines whether dispersers had higher or lower L than residents (see Figure 1, Table A1). With very short life spans, 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 & Kimura, 1970), L_R was pushed upwards (Figure 1, Season length (S) = 4 and 10), that is, 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 strongly into learning abilities (i.e., L_R). This led to a huge increase in L_R compared to learning abilities of dispersers (i.e., L_D) which were unable to exploit hard-to-access resources within their given time (Figure 1, S = 20 and 30). When increasing the total season length further, also dispersers were able to exploit hard-to-access resources (both in their natal and new settlement patches) and invested highly into L. As a result, the differences between L_R and L_D first becomes insignificant (Figure 1, Table 2, SL = 50) and then, with increased SL, reverses direction, that is, L_R becomes significantly lower than L_D (Figure 1, Table 2, $S > 50$).

Changing the timing of dispersal within the life cycle, by the parameters T_{before} and T_{after}, strongly influenced the cognitive style of disperses (Figure 2a). For a given season length, when dispersal took place in the middle of life, dispersers invested little in learning because they did not have enough time to learn either at their birthplace or in the new patch. Since this reduced the competitive abilities of dispersers, dispersal costs increased, and consequently, mean dispersal tendencies decreased (Figure 2b). However, when dispersal took place either early or late in life (e.g., breeding dispersal), then

TABLE 2 Parameter settings for simulation presented in Figure 1 main text

Abbreviation	Description	Parameter setting
A_{Ri}	Abundance of different resource types	In patch type 1: R1 = 1, R2 = 5; In patch type 2: R1 = 1, R3 = 5
C_{Ri}	Detectability of resource type i	R1 = R2 = R3 = 0.5
H_{Ri}	Handling time of resource type i	R1 = 1, R2 = R3 = 300
M	Mortality risk	0.01
$N_{Generations}$	Number of generations	300
$N_{Individuals}$	Carrying capacity of Pi	100
$N_{Patches}$	Number of patches	12
T_{after}	Length of season after dispersal	2, 4, 10, 15, 25, 50, 150, 250, 500, 1,000, 2,000
T_{before}	Length of season before dispersal	2, 4, 10, 15, 25, 50, 150, 250, 500, 1,000, 2,000
V_{Ri}	Value of resource type i	R1 = 1, R2 = R3 = 10
A	Cost coefficient of learning	1.4
M	Mutation probability	0.1
Φ	Competition factor	2
EX_{freq}	Extinction frequency (every × generation)	2
EX_N	Number of patches getting erased every EX_{freq} generation	1

TABLE 3 Parameter settings for simulation presented in Figure 2 main text

Abbreviation	Description	Parameter setting
A_{Ri}	Abundance of different resource types	In patch type 1: R1 = 1, R2 = 5, R3 = 0 In patch type 2: R1 = 1, R2 = 0, R3 = 5
C_{Ri}	Detectability of resource type i	R1 = R2 = R3 = 0.5
H_{Ri}	Handling time of resource type i	R1 = 1, R2 = R3 = 150
M	Mortality risk	0.01
$N_{Generations}$	Number of generations	500
$N_{Individuals}$	Carrying capacity of Pi	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	R1 = 1, R2 = 10
A	Cost coefficient of learning	1.4
M	Mutation probability	0.1
Φ	Competition factor	6
EX_{freq}	Extinction frequency (every × generation)	2
EX_N	Number of patches getting erased every EX_{freq} generation	1

dispersers had time to adapt to at least one set of local conditions, hence investing in L similarly to but slightly lower than residents (Figure 2a) and dispersal tendencies increased again (Figure 2b).

4 | DISCUSSION

Our model revealed strong effects of longevity and the timing of dispersal on evolved patterns in learning abilities. Sufficient longevity was needed for the evolution of high learning abilities, with dispersers needing longer life spans than residents to be able to recoup their investment into learning. Timing of dispersal modulated the relationship between learning abilities and dispersal, by determining the time dispersers had in either location (natal or settlement patch) to recoup their investment.

Similar to a previous model (Liedtke & Fromhage, 2019a), resource composition determined whether or not different cognitive styles could coexist within the same patch. That is, it is easy to find resource compositions where either all or no individuals invest strongly in learning (not shown). Coexistence, however, depends on individuals specializing on different resource types, such that some individuals specialize on more abundant and easy-to-handle resources, whereas others specialize on hard-to-access resources with higher value. Since individuals compete over these resources, negative frequency dependence stabilizes the coexistence (for a more detailed discussion, please see Liedtke & Fromhage, 2019a). For the hard-to-access resources, individuals need to invest into learning speed (L) in order to be able to learn to exploit them within the available time (i.e., life span). With very short life spans, time is not sufficient for learning and thus no investment in L occurred. Once there is enough time for learning to exploit these resources, any further increase in life span leads to a reduced investment in L

because of relaxed time pressure (i.e., individuals can reduce learning costs by learning more slowly, provided there is enough time; compare (Liedtke & Fromhage, 2019b)). This nonlinear link between life span and investment into learning speed is the underlying cause of the effect of life span on dispersal in the present model. With very short life spans, individuals do not invest in higher L and consequently residents and dispersers adopt similar cognitive styles with low learning abilities (Figure 1, leftmost data points). Yet, if life span is just long enough for learning to handle hard-to-access resources, individuals need to invest highly in L to exploit these resources. Crucially, only if fast-learning individuals encounter these resources throughout their whole life, they can recoup the investment into high L by increasing their resource intake and reproduction. So, if hard-to-access resources differ between patches, and learning progress is not transferable between resource types, then dispersers are unable to exploit hard-to-access resources either at their natal or at the settlement patch. Therefore, dispersers cannot recoup their investment into high L. Consequently, individuals investing into high L are better off staying in their natal place, and dispersers are better off investing little into L, specializing on easy-to-access resources instead (Figure 1, center).

With increased life spans the pattern reverses because, above some minimal life span, there is sufficient time for learning to handle resources both in the natal and in the settlement patch. Meanwhile, since residents only need to learn one type of hard-to-access resource, they have more time to do so and can afford to learn slower and pay less cost of L. Accordingly, dispersers have higher L than residents (Figure 1, right half). With further increase in life span, also dispersers have more time to learn and thus can likewise afford to reduce their investment in L.

A similar effect occurs when considering the timing of dispersal within the lifecycle of a species. Dispersal early in life allows

dispersers to adjust to local conditions of the settlement patch where they spend most of their life. Provided that life span is not too long (see above), this promotes the investment into L for dispersers, to a similar extent as in residents. Likewise, dispersal at the end of the lifecycle allows individuals to adjust to local conditions of the natal place where they spend most of their life. Again, this leads to minimal differences in L between residents and dispersers. If, however, dispersal takes 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. Since dispersers cannot compete with residents over hard-to-access resources, the cost of dispersal increases, and dispersal tendencies become lower. This relationship, of course, depends greatly on the species' total life span. With very short life spans, no investment in L is expected whereas with very long life span, 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.

Besides the effect of longevity on investment in learning abilities, we can observe an effect on dispersal tendencies (D) as well. With very short life spans, mean dispersal tendency is high (see $S < 20$, in Figure 1). Once a prolonged life span allows residents to exploit hard-to-access resources, the mean value of D drops considerably (see $S = 20$, in Figure 1). This pattern arises because, with short life spans, no one can learn to exploit hard-to-access resources and all individuals compete for easy-to-access resources. Consequently, residents have no (foraging) advantages over dispersers and thus dispersers can compete in new patches as well as in their natal patch. This results in low costs for dispersal and high dispersal rates. Yet, once life span is long enough to permit effective learning, residents have the advantage of being faster in exploiting hard-to-access

resources and thus outcompete dispersers, which first need to learn how to handle the new hard-to-access resources. This increases the costs of dispersal, leading to lower mean dispersal rates. Only with longer life spans, dispersers can become similarly efficient in exploiting hard-to-access resources at the settlement patch and thus are able to compete with residents. At this point, dispersal rates start to increase with longevity again ($S > 50$, in Figure 1).

Comparing our present results with those of a model without developmental plasticity (Liedtke & Fromhage, 2021), we can summarize that under both approaches a correlation between learning abilities and dispersal occurs under a wide range of environmental circumstances. Note, however, that the results of both models are in no way redundant, as biologically there is a qualitative difference between a population where dispersal and learning are correlated across habitat patches (as in Liedtke & Fromhage, 2021), and a population where dispersal and learning are phenotypically correlated even across individuals that may share the same genotype (as in the present study). Moreover, 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
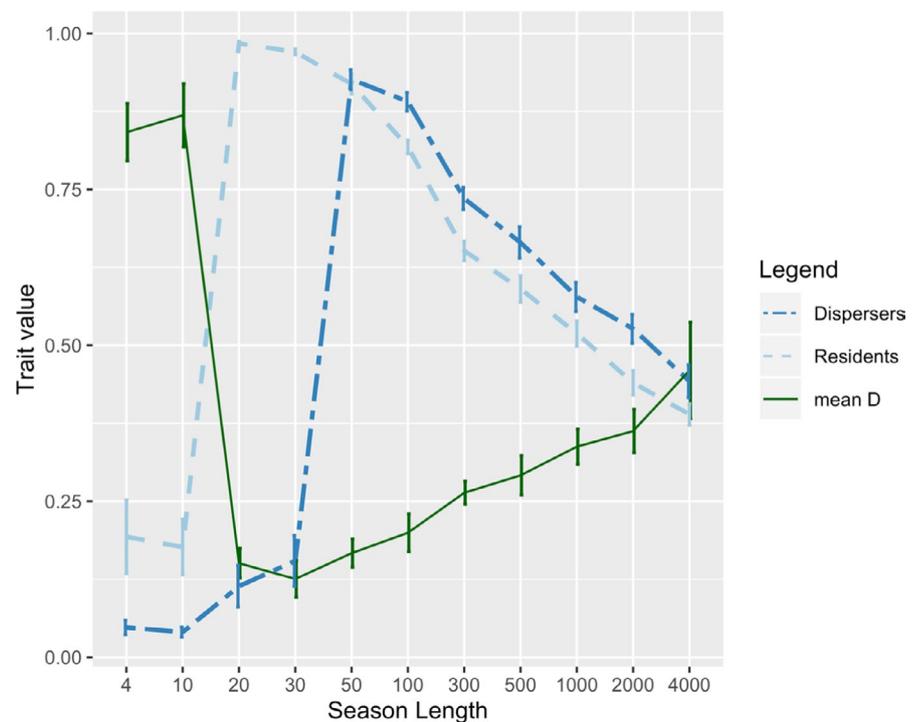
FIGURE 1 The figure shows the mean for trait values L (=learning speed) for residents (L_R), dispersers (L_D) and the population's mean dispersal tendency (mean D). Each point represents the mean of ten replicated simulation runs. In each run traits reached equilibrium well within given number of generations. Time before and after dispersal was equally long in all simulations ($T_{before} = T_{after}$). For all but one simulated season length the mean differed significantly between residents and dispersers. Error bars indicate standard deviation. For season length = 50 there was no significant difference

(a) **Learnig speed**

(b) **Dispersal tendency**
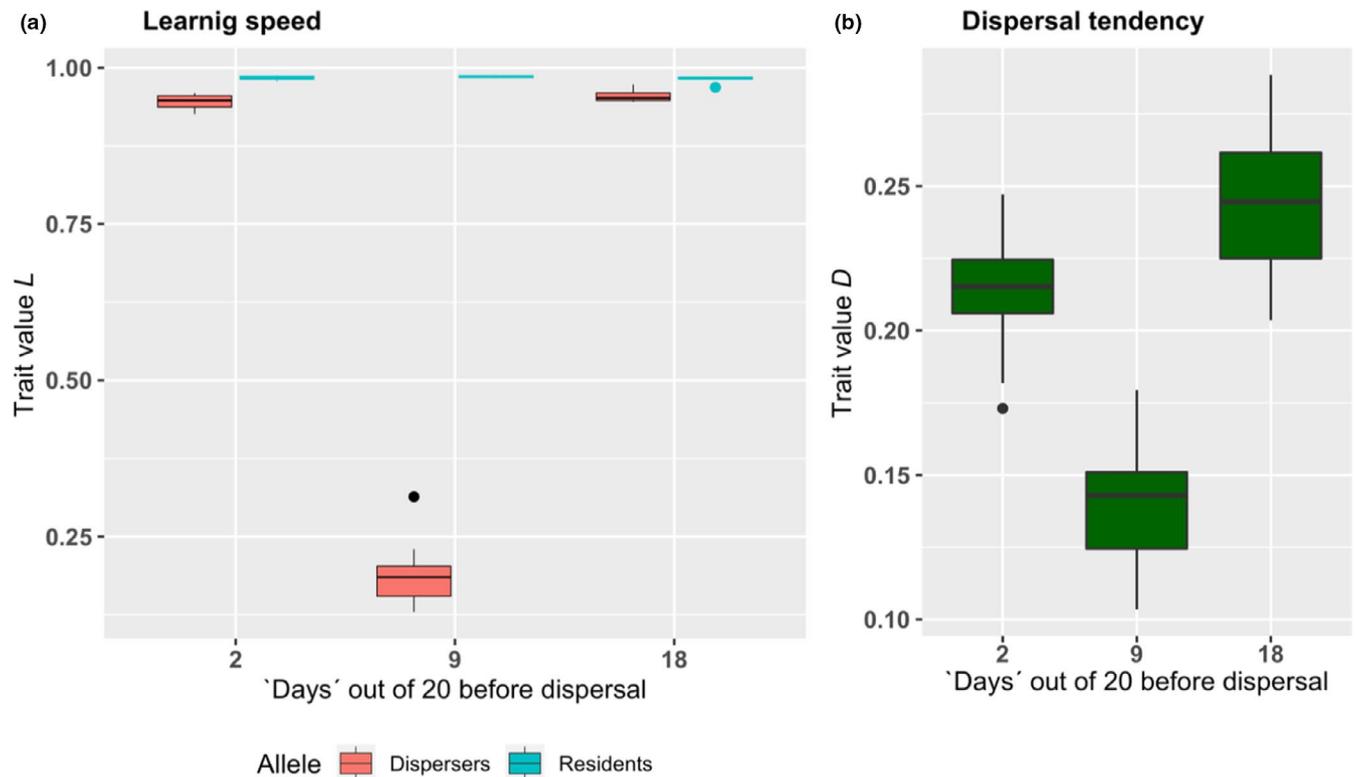
FIGURE 2 (a) Mean trait values *L* (=learning speed) for residents (L_R in blue, with matching contour colours to make colours discernible despite low variances) and dispersers (L_D in red). Note that these phenotypes are encoded by different loci, only one of which is expressed in any given individual. (b) Mean dispersal tendency of whole population. Boxplots represent the results of ten replicated runs where the mean of each simulation serves as one datapoint. The season length (i.e. in 'days') was 20 in total in each case but the time point of dispersal differed. On the left-hand side dispersal was allowed after the second, in the middle after the ninth and on the right-hand side after the 18th 'day'

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, for example, if some habitat types favor higher values in both learning ability and dispersal tendency (Liedtke & 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 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' life span 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 & Débarre, 2015).

In this study, we simulated an annual life cycle resembling short-lived species such as insects or spiders, and parameters like longevity or duration of learning a task were implemented accordingly. Yet we expect that the general principles of the interaction between learning, dispersal, and longevity will remain the same for longer-lived species such as vertebrates. The crucial point is how long individuals need to learn a task in relation to their available time as determined by their ecology. However, since learning speed should depend on the frequency with which similar tasks are encountered, it should also depend on the degree of environmental complexity and predictability. Thus, an interesting avenue for further research would be to investigate how life-history traits such as life span and timing of dispersal coevolve under variation of these environmental aspects.

CONFLICT OF INTEREST
None declared.

AUTHOR CONTRIBUTIONS
Jannis Liedtke: Conceptualization (lead); data curation (lead); funding acquisition (lead); investigation (lead); methodology (lead);

project administration (lead); validation (lead); writing–original draft (lead); writing–review and editing (equal). **Lutz Fromhage:** Conceptualization (supporting); data curation (supporting); funding acquisition (supporting); investigation (supporting); methodology (supporting); project administration (supporting); resources (supporting); supervision (lead); validation (supporting); writing–review and editing (equal).

OPEN RESEARCH BADGES

This article has been awarded <Open Data, Open Materials> Badges. All materials and data are publicly accessible via the Open Science Framework at https://doi.org/10.5061/dryad.76hdr7svb.

DATA AVAILABILITY STATEMENT

Code of simulation and data are available at Dryad Dryad DOI: https://doi.org/10.5061/dryad.76hdr7svb

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REFERENCES

Alem, S., Perry, C. J., Zhu, X., Loukola, O. J., Ingraham, T., Søvik, E., & Chittka, L. (2016). Associative mechanisms allow for social learning and cultural transmission of string pulling in an insect. *PLoS Biology*, *14*(10), e1002564. https://doi.org/10.1371/journal.pbio.1002564

Boesch, C., Bombjaková, D., Meier, A., & Mundry, R. (2019). Learning curves and teaching when acquiring nut-cracking in humans and chimpanzees. *Scientific Reports*, *9*(1), 1515. https://doi.org/10.1038/s41598-018-38392-8

Bonte, D., & de la Pena, E. (2009). Evolution of body condition-dependent dispersal in metapopulations. *Journal of Evolutionary Biology*, *22*, 1242–1251. https://doi.org/10.1111/j.1420-9101.2009.01737.x

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T. G., Chaput-Bardy, A., Clobert, J., Dytham, C., … Travis, J. M. J. (2012). Costs of dispersal. *Biological Reviews*, *87*(2), 290–312. https://doi.org/10.1111/j.1469-185X.2011.00201.x

Boogert, N. J., Madden, J. R., Morand-Ferron, J., & Thornton, A. (2018). Measuring and understanding individual differences in cognition. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *373*(1756), 20170280. https://doi.org/10.1098/rstb.2017.0280

Bowler, D. E., & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. *Biological Reviews*, *80*, 205–225. https://doi.org/10.1017/s1464793104006645

Cauchoix, M., Chow, P. K. Y., van Horik, J. O., Atance, C. M., Barbeau, E. J., Barragan-Jason, G., Bize, P., Boussard, A., Buechel, S. D., Cabirol, A., Cauchard, L., Claidière, N., Dalesman, S., Devaud, J. M., Didic, M., Doligez, B., Fagot, J., Fichtel, C., Henke-von der Malsburg, J., … Morand-Ferron, J. (2018). The repeatability of cognitive performance: A meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170281. https://doi.org/10.1098/rstb.2017.0281

Clobert, J., Galliard, J.-F.-L., Cote, J., Meylan, S., & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, *12*(3), 197–209. https://doi.org/10.1111/j.1461-0248.2008.01267.x

Cote, J., Bestion, E., Jacob, S., Travis, J., Legrand, D., & Baguette, M. (2017). Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. *Ecography*, *40*(1), 56–73. https://doi.org/10.1111/ecog.02538

Cote, J., & Clobert, J. (2012). *Dispersal syndromes in the common lizard: Personality traits, information use, and context-dependent dispersal decisions*. Oxford Univ Press.

Crow, J. F., & Kimura, M. (1970). *An introduction to population genetics theory*. An introduction to population genetics theory.

Deaner, R. O., Barton, R. A., & van Schaik, C. P. (2003). Primate brains and life histories: Renewing the connection. In P. M. Kappeler, & M. E. Pereira (Eds.), *Primate life histories and socioecology* (pp. 233–265). The University of Chicago Press.

Delgado, M. M., Bartoń, K. A., Bonte, D., & Travis, J. M. J. (2014). Prospecting and dispersal: Their eco-evolutionary dynamics and implications for population patterns. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1778), 20132851. https://doi.org/10.1098/rspb.2013.2851

Edelaar, P., Jovani, R., & Gomez-Mestre, I. (2017). Should I change or should I go? Phenotypic plasticity and matching habitat choice in the adaptation to environmental heterogeneity. *The American Naturalist*, *190*(4), 506–520. https://doi.org/10.1086/693345

Geffroy, B., Sadoul, B., Putman, B. J., Berger-Tal, O., Garamszegi, L. Z., Møller, A. P., & Blumstein, D. T. (2020). Evolutionary dynamics in the Anthropocene: Life history and intensity of human contact shape antipredator responses. *PLoS Biology*, *18*(9), e3000818. https://doi.org/10.1371/journal.pbio.3000818

Guinet, C., & Bouvier, J. (1995). Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Canadian Journal of Zoology*, *73*(1), 27–33. https://doi.org/10.1139/z95-004

Gyllenberg, M., Kisdi, E., & Utz, M. (2008). Evolution of condition-dependent dispersal under kin competition. *Journal of Mathematical Biology*, *57*, 285–307. https://doi.org/10.1007/s00285-008-0158-2

Kenward, B., Rutz, C., Weir, A. A. S., & Kacelnik, A. (2006). Development of tool use in New Caledonian crows: Inherited action patterns and social influences. *Animal Behaviour*, *72*(6), 1329–1343. https://doi.org/10.1016/j.anbehav.2006.04.007

Legrand, D., Larranaga, N., Bertrand, R., Ducatez, S., Calvez, O., Stevens, V. M., & Baguette, M. (2016). Evolution of a butterfly dispersal syndrome. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20161533. https://doi.org/10.1098/rspb.2016.1533

Liedtke, J., & Fromhage, L. (2019a). Modelling the evolution of cognitive styles. *BMC Evolutionary Biology*, *19*(1), 234. https://doi.org/10.1186/s12862-019-1565-2

Liedtke, J., & Fromhage, L. (2019b). Need for speed: Short lifespan selects for increased learning ability. *Scientific Reports*, *9*(1), 1–6. https://doi.org/10.1038/s41598-019-51652-5

Liedtke, J., & Fromhage, L. (2021). The joint evolution of learning and dispersal maintains intraspecific diversity in metapopulations. *Oikos*, *130*, 808–818. https://doi.org/10.1111/oik.08208

Liedtke, J., & Schneider, J. M. (2014). Association and reversal learning abilities in a jumping spider. *Behavioural Processes*, *103*, 192–198. https://doi.org/10.1016/j.beproc.2013.12.015

Maspons, J., Molowny-Horas, R., & Sol, D. (2019). Behaviour, life history and persistence in novel environments. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1781), 20180056. https://doi.org/10.1098/rstb.2018.0056

Massol, F., & Débarre, F. (2015). Evolution of dispersal in spatially and temporally variable environments: The importance of life cycles. *Evolution*, *69*(7), 1925–1937. https://doi.org/10.1111/evo.12699

McNamara, J. M., & Dall, S. R. X. (2011). The evolution of unconditional strategies via the "multiplier effect". *Ecology Letters*, 14, 237–243. https://doi.org/10.1111/j.1461-0248.2010.01576.x

Mettke-Hofmann, C., Wink, M., Winkler, H., & Leisler, B. (2005). Exploration of environmental changes relates to lifestyle. *Behavioral Ecology*, 16(1), 247–254. https://doi.org/10.1093/beheco/arh159

Niven, J. E., & Laughlin, S. B. (2008). Energy limitation as a selective pressure on the evolution of sensory systems. *Journal of Experimental Biology*, 211(11), 1792–1804. https://doi.org/10.1242/jeb.017574

O'Riain, M. J., Jarvis, J. U. M., & Faulkes, C. G. (1996). A dispersive morph in the naked mole-rat. *Nature*, 380(6575), 619–621. https://doi.org/10.1038/380619a0

Poethke, H. J., Hovestadt, T., Mitesser, O., & Perrin, A. E. N. (2003). Local extinction and the evolution of dispersal rates: Causes and correlations. *The American Naturalist*, 161(4), 631–640. https://doi.org/10.1086/368224

Roff, D. A. (1986). The evolution of wing dimorphism in insects. *Evolution*, 40(5), 1009–1020. https://doi.org/10.1111/j.1558-5646.1986.tb00568.x

Sasakura, H., & Mori, I. (2013). Behavioral plasticity, learning, and memory in *C. elegans*. *Current Opinion in Neurobiology*, 23(1), 92–99. https://doi.org/10.1016/j.conb.2012.09.005

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *Quarterly Review of Biology*, 79(3), 241–277. https://doi.org/10.1086/422893

Sol, D. (2009). The cognitive-buffer hypothesis for the evolution of large brains. In R. Dukas, & J. M. Ratcliffe (Eds.), *Cognitive ecology II* (pp. 111–134). The University of Chicago Press.

Toor, I., Edwards, P. D., Kaka, N., Whitney, R., Ziolkowski, J., Monks, D. A., & Holmes, M. M. (2020). Aggression and motivation to disperse in eusocial naked mole-rats, *Heterocephalus glaber*. *Animal Behaviour*, 168, 45–58. https://doi.org/10.1016/j.anbehav.2020.07.022

Van Belleghem, S. M., & Hendrickx, F. (2014). A tight association in two genetically unlinked dispersal related traits in sympatric and allopatric salt marsh beetle populations. *Genetica*, 142(1), 1–9. https://doi.org/10.1007/s10709-013-9749-y

APPENDIX

Season length (S)	t	df	p-value	Mean L resident	Mean L disperser
4	7.5912	9	3.36E−05	0.1933035	0.04778159
10	8.5109	9	1.35E−05	0.1767255	0.04029792
20	81.259	9	3.28E−14	0.9840266	0.1138525
30	63.587	9	2.97E−13	0.9704485	0.1546901
50	−1.3462	9	0.2112	0.91882	0.9261572
100	−16.464	9	5.01E−08	0.8181473	0.890475
300	−11.524	9	1.09E−06	0.6514239	0.7353187
500	−5.6239	9	0.0003242	0.5903464	0.6647682
1,000	−5.0862	9	0.0006573	0.5188527	0.5776454
2,000	−8.6489	9	1.18E−05	0.4399097	0.5263899
4,000	−4.7635	9	0.001025	0.3893362	0.4423997

TABLE A1 Results of paired *t*-tests comparing mean values of learning abilities (*L*) of residents and dispersers

Note: Separately for each season length (*S* = 4 to 4,000) the mean values of *L* of residents and dispersers of each replicated simulation (10 runs per *S*) were used as datapoints.