

## Information processing in models for density-dependent emigration: A comparison

Thomas Hovestadt<sup>\*,1</sup>, Alexander Kubisch, Hans-Joachim Poethke

University of Würzburg, Biozentrum, Field Station Fabrikshleichach, Glashüttenstrasse 5, 96181 Rauhenbrach, Germany

### ARTICLE INFO

#### Article history:

Received 11 March 2009  
Received in revised form 22 October 2009  
Accepted 5 November 2009  
Available online 5 December 2009

#### Keywords:

Individual-based simulation  
Density-dependent dispersal  
Information processing  
Evolutionary contest

### ABSTRACT

Density-dependent emigration has been recognized as a fitness enhancing strategy. Yet, especially in the modelling literature there is no consensus about how density-dependent emigration should quantitatively be incorporated into metapopulation models. In this paper we compare the performance of five different dispersal strategies (defined by the functional link between density and emigration probability). Four of these strategies are based on published functional relationships between local population density and emigration probability, one assumes density-independent dispersal. We use individual-based simulations of time-discrete metapopulation dynamics and conduct evolution experiments for a broad range of values for dispersal mortality and environmental stochasticity. For each set of these conditions we analyze the evolution of emigration rates in 'monoculture experiments' (with only one type of dispersal strategy used by all individuals in the metapopulation) as well as in selection experiments that allow a pair-wise comparison of the performance of each functional type. We find that a single-parameter 'asymptotic threshold' strategy – derived from the marginal value theorem – with a decelerating increase of emigration rate with increasing population density, out-competes any other strategy, i.e. density-independent emigration, a 'linear threshold' strategy and a flexible three-parameter strategy. Only when environmental conditions select for extremely high emigration probabilities (close to one), strategies may perform approximately equally. A simple threshold strategy derived for the case of continuous population growth performs even worse than the density-independent strategy. As the functional type of the dispersal function implemented in metapopulation models may severely affect predictions concerning the survival of populations, range expansion, or community changes we clearly recommend to carefully select adequate functions to model density-dependent dispersal.

© 2009 Elsevier B.V. All rights reserved.

### 1. Introduction

Dispersal has been recognized as an ecological key process and has attracted the interest of a growing number of empirical as well as theoretical ecologists (Clobert et al., 2001; Bullock et al., 2002). Dispersal can influence community structure (e.g. Clark et al., 1999; Levine and Murrell, 2003; Holyoak et al., 2005; Zobel et al., 2005; Cadotte, 2006) and the persistence of (meta-)populations (e.g. Frank and Wissel, 1998; Brachet et al., 1999). Yet, metapopulation models often assume that dispersal is a completely random event (e.g. Hanski, 1999). Dispersal decisions (more accurately we should talk about the movement decisions underlying dispersal), however, have far reaching consequences for individuals' (inclusive) fitness. Consequently, the (movement) rules according to which these deci-

sions are taken presumably underlie strong selective pressure. Specifically, natural selection should favour individuals who take conditional dispersal decisions (Bowler and Benton, 2005), i.e. use available information about the environment to 'fine-tune' dispersal decisions in an adaptive way (Getz and Saltz, 2008; Nathan et al., 2008; Clobert et al., 2009).

An obvious case of an adaptive dispersal strategy would be emigration from populations with intense competition over some critical resources, i.e. emigration from high-density localities. There is indeed considerable empirical evidence that population density does affect emigration (Herzig, 1995; Conradt et al., 2000; Kindlmann et al., 2004; Morris and Diffendorfer, 2004; Enfjäll and Leimar, 2005; Matthysen, 2005). Accounting for such density-dependent dispersal in metapopulation models has, for example, a substantial effect on predictions concerning the dynamics and survival of metapopulations (e.g. Johst and Brandl, 1997; Ruxton and Rohani, 1998; Hovestadt and Poethke, 2006).

Just recognizing, however, that population density or habitat quality in general should affect emigration decisions is not enough. What we need doing is defining the adequate quantitative link

<sup>\*</sup> Corresponding author. Tel.: +49 931 3183083; fax: +49 931 3183089.

E-mail address: [hovestadt@biozentrum.uni-wuerzburg.de](mailto:hovestadt@biozentrum.uni-wuerzburg.de) (T. Hovestadt).

<sup>1</sup> Muséum National d'Histoire Naturelle, CNRS UMR 7179, 1 Avenue du Petit Château, 91800 Brunoy, France.

between population density and emigration decisions. This is a question of both, practical and theoretical relevance. In empirical studies it has, to our knowledge, never been attempted to distinguish between different functional relationships between population density and emigration (or movement activity); given the imprecision of data measurement this is, however, not very surprising.

More puzzling, in the modelling literature plurality exists in the way how density-dependent emigration (the ‘dispersal strategy’) has been incorporated into patch-matrix models, even in models, which otherwise follow completely identical assumptions. Yet, other than theoreticians, the modelling community has not reflected much upon the validity of the different approaches. In our view, it is thus time to critically evaluate justification and usefulness of these different approaches in an evolutionary context.

In this paper we use individual-based simulations of a metapopulation consisting of discrete local populations with non-overlapping generations linked by dispersal to evaluate the performance of four different functions for density-dependent ‘emigration rules’. One assumption to be tested is that parameter rich – and thus flexible – strategies allow a better ‘fine-tuning’ of emigration rates to the specific environmental conditions than parameter-poor strategies. Yet, it may also be argued that it takes more time to select multiple-parameter strategies to their optimal shape so that parameter-poor strategies could perform better in an evolutionary context. In this paper we will compare the evolution of selected functions for density-dependent emigration that have been proposed in the modelling literature. The analysis we perform here is, however, an exemplary one valid for a certain type of population model. Our specific conclusions should not directly be transferred to systems that follow a completely different population dynamics.

We will analyze the influence of these functions on emigration rates in ‘monoculture experiments’ as well as in selection experiments that allow a pair-wise comparison of the performance of each function. Based on our results we will give a recommendation, which dispersal function is the most adequate for implementation in metapopulation models of species with discrete generations like insects. This is at the same time also a call to empiricists to more carefully evaluate the quantitative relationship between population density and emigration.

## 2. Methods

### 2.1. Population model

In all our individual-based simulation experiments we assume a metapopulation of  $n = 100$  discrete habitat patches with equal carrying capacity ( $K = 100$ ). Locally, the growth of the population (haploid and annual organisms) in patch  $i$  follows a time-discrete logistic function according to a simplified model suggested by Maynard-Smith and Slatkin (1973) and Hassell (1998) and successfully fitted to the data of many insect populations (Bellows, 1981):

$$N_{i,t+1} = N_{i,t} \Lambda_{i,t} s \quad \text{with} \quad s = \frac{1}{1 + a N_{i,t}} \quad \text{and} \quad a = \frac{\lambda - 1}{K_i} \quad (1)$$

In this model,  $N_{i,t}$  and  $N_{i,t+1}$  are the population sizes in patch  $i$  in year  $t$  and  $t + 1$  respectively.  $\Lambda_{i,t}$  is the patch specific growth rate drawn separately for each patch and each time step from a log-normal distribution with mean  $\lambda$  and environmental variance  $\sigma^2$ . Implicitly, we thus assume spatially and temporally uncorrelated variability in population growth rates. Within each patch the new generation is produced by first drawing for each individual a random number of offspring from a Poisson distribution with mean  $\Lambda_{i,t}$ . These offspring then survive to maturity with probability  $s$  as given in Eq.

(1). Surviving offspring may then emigrate according to their individual, genetically determined dispersal strategy (see below). All individuals take their emigration decision simultaneously. Emigration incurs a cost, which is implemented as dispersal mortality ( $\mu$ ). That is, emigrating individuals die with probability  $\mu$  independent of patch origin. The surviving  $(1 - \mu)$  emigrants are randomly distributed over all non-natal patches, i.e. we assume ‘global dispersal’. This life-cycle is repeated until the maximum simulation time  $T$  is reached. More details on the implication of this model can be found in (Poethke and Hovestadt, 2002). The identical population model was also implemented by e.g. Travis and Dytham (1998), Ruxton and Rohani (1998), or Kun and Scheuring (2006).

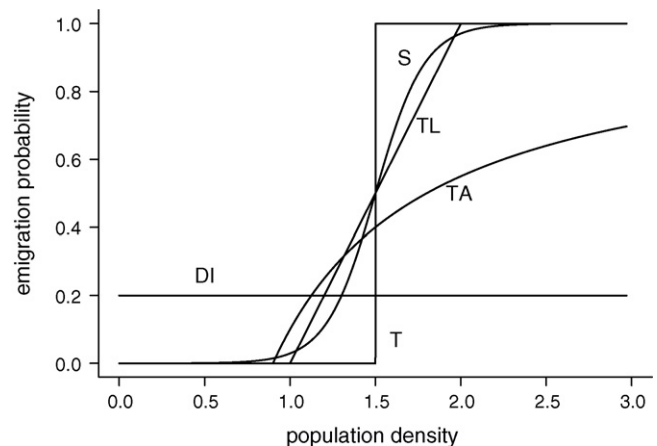
### 2.2. Emigration strategy and inheritance

The emigration decisions of an individual fall according to the specific dispersal strategy coded in the individual’s ‘genome’. One gene is responsible for the dispersal strategy as such, while – depending on the strategy – up to three additional ‘parameter genes’ quantitatively determine the emigration propensity of an individual (see below). Each individual inherits its genes from its mother. However, in the course of inheritance parameter genes may mutate (but not the strategy gene!) with small probability  $m = 0.001$ . In case that a mutation occurs, the value of the affected gene is modified by addition of a random number drawn from a normal distribution with a mean of zero and a standard deviation of 0.2.

In our simulation experiments we implemented four different functions for density-dependent emigration strategies. As the implementation of density-independent emigration is still standard practice in metapopulation modelling we additionally include the case of density-independent emigration into our comparison. In all cases, the genetic traits of an individual define the probability of its emigration; except for the case of density-independent emigration this probability is always modulated by local population density. Whether an individual ultimately emigrates is a stochastic decision: the individual emigrates if a number drawn from uniform probability distribution  $[0 \dots 1]$  is smaller than the emigration probability estimated for that individual. The five different strategies implemented Fig. 1 are defined as follows:

(a) Density-independent emigration (DI).

$$p_{DI}(N_t) = d = \text{const} \quad (2a)$$



**Fig. 1.** Plot of the different functional relationships between population density ( $N/K$ ) and emigration probability implemented in this paper. DI: density independent, T: simple threshold, TA: threshold-asymptotic, TL: threshold-linear, and S: sigmoid. Curves of functions are drawn with the parameter values used at initialization of ‘monoculture experiments’ (see text).

i.e. the gene of an individual directly codes for its emigration probability independent of the population density in its natal patch. The only evolving parameter is  $d$ .

- (b) Linear threshold model (Travis et al., 1999) (TL). Travis et al. have suggested the use of a simple threshold model according to which emigration should not occur as long population density is below a certain threshold and grow linearly with density from then on:

$$p_{TL}(N_t) = \begin{cases} 0 & \text{for } I + s \frac{N_t}{K} < 0 \\ I + s \frac{N_t}{K} & \text{for } 0 \leq I + s \frac{N_t}{K} \leq 1 \\ 1 & \text{for } I + s \frac{N_t}{K} > 1 \end{cases} \quad (2b)$$

i.e. emigration probability is calculated according to a linear equation with intercept  $I$ , and slope  $s$  as evolving parameters. Travis et al. have discussed the benefits of density-dependent emigration and argued for the presence of a threshold density below which emigration should not occur. Yet they selected this specific functional relationship for its simplicity and ease of implementation.

- (c) Sigmoid model (Kun and Scheuring, 2006) (S). Kun and Scheuring introduced a functional relationship between population density and emigration that would usually look sigmoid (S-shaped):

$$p_S(N_t) = \frac{D_0}{1 - \exp(-\alpha(\frac{N_t}{K} - \beta))} \quad (2c)$$

Emigration probability is thus determined by three evolving parameters ( $D_0$ ,  $\alpha$ , and  $\beta$ ).  $D_0$  specifies the maximum emigration probability to be reached,  $\alpha$  the 'rapidity' with which the emigration probability increases with increasing population density, and  $\beta$  the inflection point, i.e. the density at which the emigration probability reaches half its maximum value  $D_0$ .

The equation suggested is fundamentally very flexible and would also allow for the evolution of density-independent or even inversely density-dependent emigration. Kun and Scheuring have, however, not given any theoretical arguments for this functional relationship between density and emigration probability.

- (d) Asymptotic threshold model (Ruxton and Rohani, 1998; Poethke and Hovestadt, 2002) (TA). Based on arguments rooted in the marginal value theorem (Charnov, 1976). The model predicts that emigration only occurs if density is larger than the evolving threshold value  $C_{TA}$  and emigration probability then increases asymptotically towards one.

$$p_{TA}(N_t) = \begin{cases} 0 & \text{if } C_{TA} \geq \frac{N_t}{K} \\ 1 - \frac{C_{TA}}{N_t/K} & \text{if } C_{TA} < \frac{N_t}{K} \end{cases} \quad (2d)$$

The function has the property that individuals emigrate in such proportion that population density remains at  $N_t/K = C_{TA}$  (before immigration).

- (e) Threshold model (Metz and Gyllenberg, 2001) (T). According to this model, an individual stays at home as long as population density remains below the genetically determined threshold density  $C_T$ , and emigrates with certainty, if population density is above that threshold:

$$p_T(N_t) = \begin{cases} 0 & \text{if } \frac{N_t}{K} \leq C_T \\ 1 & \text{if } \frac{N_t}{K} > C_T \end{cases} \quad (2e)$$

The theoretical derivation of this model is based on the same arguments as the previous one, but applies in the case of con-

tinuous population growth and dispersal, i.e. any individual 'decides' to emigrate at a unique moment in time. In that case, an individual should emigrate with certainty ( $p_T = 1$ ) as soon as its fitness expectations at home are lower than those expected if it disperses and stay at home otherwise.

Note that the dispersal strategies DI, T, and TA are governed by one evolving parameter, TL by two, and S by three parameters.

### 2.3. Simulation experiments

We carried out two sets of simulation experiments. In the first we analyzed the evolution of parameters in a given environmental setting for each strategy separately. Evolution in these 'monoculture experiments' was simulated for each of the five strategy types over a period of 10 000 time steps for each combination of dispersal mortality ( $\mu$ ) and environmental variability ( $\sigma$ ) as listed below. Simulations were initialized by placing  $K$  individuals with identical strategy parameters into each habitat patch. The initial parameters for the different strategy types were DI:  $d = 0.2$ ; TL:  $I = -1$ ,  $s = 1$ ; S:  $D_0 = 1$ ,  $\alpha = 7$ ,  $\beta = 1.5$ ; TA:  $C_{TH} = 0.9$ ; T:  $C_T = 1.5$ .

The simulation experiments showed that for any strategy 10 000 time steps were more than sufficient to reach a stable equilibrium in the distribution of dispersal parameters in the metapopulation. After this time, the resulting parameter values for each individual were saved for further use in the following set of competition experiments.

In the 'competition experiments' we analyzed the success of all strategy types in direct pair-wise contests. These simulations were initialized by randomly taking 50% of the individuals from each of two different strategy types to generate a mixed population. Individuals with their traits were randomly chosen from the list of individuals that had been stored at the end of the monoculture experiments; simulations were thus initialized with a variable population for both dispersal types. An experiment was terminated if one strategy achieved dominance (more than 95% of all individuals). If this did not happen within 10 000 time steps so that no winner could be identified, a 'draw' was noted as the outcome of this competition experiment.

Previous studies (Travis et al., 1999; Poethke and Hovestadt, 2002; Poethke et al., 2003; Kun and Scheuring, 2006) have shown that dispersal mortality ( $\mu$ ) and environmental variability ( $\sigma$ ) have a strong influence on the evolution of emigration probabilities (the emergent phenotype). In contrast (Travis et al., 1999) and our own explorative simulations have show that variation of habitat capacity is of minor importance for simulation results if it is large enough so that demographic stochasticity becomes negligible. We thus fix habitat capacity at  $K = 100$  for all patches, and mean population growth at  $\lambda = 2$  throughout all simulation experiments. However, we performed simulation experiments for all possible combinations of environmental fluctuation  $\sigma \in \{0, 0.2, 0.5, 1.0\}$  and dispersal mortality  $\mu \in \{0, 0.05, 0.1, 0.2, 0.5, 0.8, 0.95\}$ . For each of these combinations and each of all pair-wise combinations of dispersal types simulation experiments were replicated 50 times. In total we thus performed  $4(\sigma) \times 7(\mu) \times 50(\text{replicates}) = 1400$  competition experiments for each possible combination (10 in total) of two emigration strategies.

For each simulation run, we recorded the final parameter distribution among individuals (separately for each strategy), the mean emigration probability recorded over the last 1000 simulation steps (again separately for each strategy), and, in the pair-wise competition experiments, which strategy won the competition and at what time step the simulation was terminated. For the numerical and graphical presentation of data, we used the R language for statistical computing (version 2.7), distributed under the GNU General

Public License, Version 2, June 1991 (R Development Core Team, 2007).

3. Results

Whatever the emigration strategy, we observe a clear decline of the emerging mean emigration probability (the ‘phenotype’) with increasing mortality costs ( $\mu$ ) and an increase in emigration as environmental variability ( $\sigma$ ) increases. As such, these findings are not new (Travis et al., 1999; Poethke and Hovestadt, 2002; Bach et al., 2007) and demonstrating this is not our primary concern here. More importantly, in the monoculture experiments all strategies evolve towards approximately similar emigration probabilities under similar environmental conditions (Fig. 2). Yet, under conditions favouring substantial dispersal (low  $\mu$ , high  $\sigma$ ) there is a consistent difference in emigration between strategies. Generally, the DI strategy and the simple threshold strategy (T) evolve towards somewhat higher emigration probabilities than the other three strategies.

In the competition experiments the TA strategy always replaced the other strategies except under conditions that either select for very low emigration (high dispersal mortality and low environmental variability; Table 1) or for an emigration probability close to one (dispersal mortality  $\mu = 0$  or 0.05; not included in Table 1). In these cases results were often ambiguous with many draws and no clear winning strategy. Otherwise, the replacement of other strategies usually took place rather quickly, especially in scenarios with high environmental variability ( $\sigma$ ); in the later case replacement took usually less than 500 time steps, sometimes even in less than 100 time steps. The second best strategy was strategy S followed by TL. It is noteworthy that the simple threshold model T performed

Table 1  
Outcome of competition experiments.

Environmental variability ( $\sigma$ )		
Disp. mort ( $\mu$ )	0	0.2
0.1	TA $\gg$ S $\geq$ TL $\gg$ DI $\gg$ T	TA $\gg$ S = TL $\gg$ DI = T
0.2	TA $\gg$ S $>$ TL $\gg$ DI $\gg$ T	TA $\gg$ S $>$ TL $\gg$ DI = T
0.5	TA $\geq$ S $\gg$ TL $<$ DI $\gg$ T	TA $\gg$ S $>$ TL $\gg$ DI $\gg$ T
0.8	S = TA = TL $>$ DI = T <sup>a</sup>	TA = S $\gg$ TL $>$ DI = T <sup>b</sup>
0.95	TA = S = TL = DI = T	TA = S = TL = DI = T
	0.5	1
0.1	TA $\gg$ S $>$ TL $\gg$ DI = T	TA $\gg$ S = TL $\gg$ T = DI
0.2	TA $\gg$ S $>$ TL $\gg$ DI = T	TA $\gg$ S = TL $\gg$ T $\geq$ DI
0.5	TA $\gg$ S $\gg$ TL $\gg$ DI = T	TA $\gg$ S $>$ TL $\gg$ T $\gg$ DI
0.8	TA $\gg$ S $\gg$ TL $\gg$ DI = T	TA $\gg$ S $\gg$ TL $\gg$ T $\gg$ DI
0.95	TA $\geq$ S $\gg$ TL $\gg$ DI $\gg$ T	TA $>$ S $\gg$ TL $\gg$ T $\gg$ DI

In each cell we give the ranking (always linear) of the different strategies. Symbols used indicate: ‘ $\gg$ ’ out-competed the other strategies in at least 45 of 50 contests, ‘ $>$ ’ in 31–44 of the simulations, ‘ $\geq$ ’ at least twice as many wins than losses, at least 20 draws, ‘=’ no decisive ranking (more than 30 draws and/or about equal number of wins and losses). Results for very low dispersal mortality ( $\mu = 0, 0.05$ ) are not included, as they generally do not show a decisive ranking.

<sup>a</sup> Only S out-competes DI and T.  
<sup>b</sup> S  $\geq$  TL.

even worse than the density-independent strategy except for the scenarios with the highest environmental variability.

4. Discussion

In our simulations we used a rather broad spectrum of structurally different strategy types but nonetheless, for any given combination of environmental variability ( $\sigma$ ) and dispersal mortality ( $\mu$ ), all strategies lead to approximately similar mean

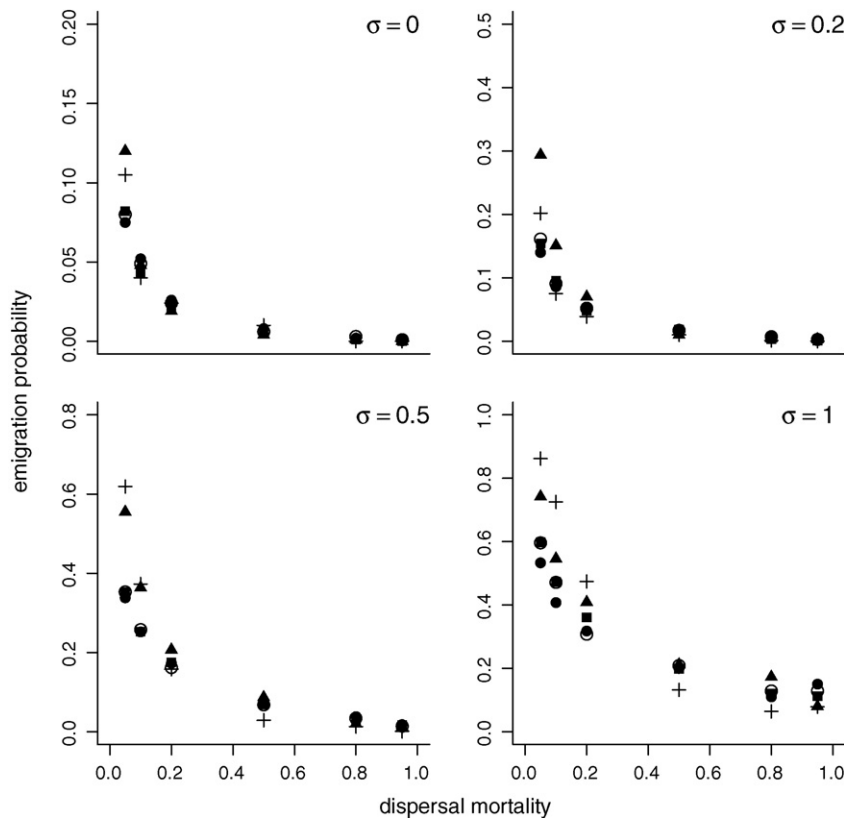


Fig. 2. Effect of dispersal mortality ( $\mu$ ) and environmental variability ( $\sigma$ ) on the evolving emigration probability for the five different dispersal strategies (cross: strategy DI, circle: S, filled square: TL, dot: TA, and filled triangle: T). Results are mean values over the last 1000 time steps from the monoculture experiments (single runs), i.e. simulations where each strategy evolved independently from the others. Note the different scaling of the y-axis. With a dispersal mortality of 0 emigration probabilities evolved towards 1 for all strategies. To enhance clarity we have not included these data points into the graph.



emigration probabilities if they evolved independently from each other. However, there are consistent differences between strategies. Under conditions that generally favour high emigration, density-independent emigration (DI) usually results in higher emigration probabilities than the conditional strategies (TL, TA, and S) that take the information about local population density into account. This may appear counterintuitive but the latter strategies are more 'efficient', i.e. require fewer dispersal events, in driving the metapopulation towards an ideal-free distribution (Enfjäll and Leimar, 2009).

Our simulation results clearly show that a simple correlation between strategy flexibility, i.e. parameter number, and competitive success does not exist. Instead the overall winning strategy is the single-parameter strategy TA. The only ambiguities occurred under conditions that either favour (nearly) complete dispersal, i.e. with dispersal mortality close to zero, or conditions, which strongly select against emigration. As parameters can be adjusted for all functions to generate an emigration probability of one, most competition experiments ended in a draw in the first case. This is not surprising as with such high emigration probability, density-dependent dispersal does obviously not constitute and added benefit—the information about density becomes rather worthless. Under conditions strongly selecting against dispersal (high dispersal mortality and low environmental variability) all strategies evolve towards very low emigration probabilities, i.e. emigration at very high densities only. In this case evolution underlies considerable randomness and selection progresses only slowly because density-conditions rarely fall into regions where the subtle differences between strategies become noticeable and are exposed to selection. Consequently, many competition experiments ended with a draw; yet a winning strategy would presumably emerge in longer simulation runs.

Even though we have included a fair spectrum of (reasonable) strategies in our 'tournament', there could be further candidate functions linking population density to emigration probability. For example, Johst and Brandl (1997) have implemented a dispersal strategy with an exponential increase in emigration probability as population density increases. Yet, based on the evidence presented here this strategy is likely to perform poorly in competition with the strategies tested, as it is a function with an accelerating increase in emigration probability, where the optimal strategy (TA) demands a decelerating increase. The working group of Lars Bach published still another model of density-dependent dispersal (Bach et al., 2007). They assumed that the evolution of dispersal depends on the ratio of the density in the prospective target patch and the natal patch. This requires, however, that an animal could collect information about the population density in a number (at least two) of different patches. This is likely to be possible only if movement is so cheap that individuals can first explore the quality of different potential target sites before taking the decision to settle in one of them. Because the model is structurally different from the others and rather addresses an optimal-foraging problem, we have not included this model in our comparison.

Of the five functions defining the link between population density and emigration probability (Eq. (2a)–(2e)) the TA model is the only one with a sound theoretical justification applicable to the discrete life-cycle we implement in our simulations (Lemel et al., 1997; see also Holt and Barfield, 2001; Poethke and Hovestadt, 2002). The function is based on the fundamental idea that in populations regulated by competition emigration must be frequency-dependent. The derivation of the model is routed in the marginal value theorem (Charnov, 1976) yet acknowledges that individuals do not have information about population density in non-natal target sites. Thus a global ideal-free distribution cannot be achieved (Ranta et al., 1999). However – ignoring kin-effects (see Poethke et al., 2007) – fitness expectations of individuals emigrating from a certain patch

should be identical to that of philopatric individuals in the same patch.

The failure of the simple T strategy (Metz and Gyllenberg, 2001) in most of our experiments does not devalue its underlying theory, which is fundamentally the same as that of the winning strategy TA. In fact, the outcome was expectable as the specific arguments used in its derivation only apply for the case of continuous population growth where dispersal decisions are not taken synchronously within a population. We thus implemented it here into a simulation model, which simply did not meet the underlying assumptions of the theory. In fact, in a discrete population model the strategy generates pathologic dynamics as all individuals of a population emigrate as soon as the threshold density is reached, leaving an empty patch behind. However, T should turn out to be the winning strategy in simulations with continuous population growth where each individual takes its emigration decisions at a different moment in time. We have generated confirming evidence for this prediction in preliminary simulation experiments.

It is known, that spatial heterogeneity, i.e. variability in patch capacities, also affects the outcome of dispersal evolution (McPeck and Holt, 1992; Travis, 2001), as does the type of density regulation (Holt and McPeck, 1996; Johst et al., 1999). Indeed, the two strategies T and TA also account for the effect of habitat heterogeneity on emigration decisions in their original versions (Metz and Gyllenberg, 2001; Poethke and Hovestadt, 2002). Because the other functions tested in this 'contests' (TL and S) did not account for such patch size effects, we used simplified versions of the two models here. Yet, according to the original versions of the TA and T model patch capacity does not change the functional relationship between population density and emigration probability fundamentally; patch capacity only alters the location of the threshold density, at which to emigrate from a patch (at lower density from smaller patches). We thus believe, that the conclusions we draw would also hold for simulations incorporating habitat heterogeneity.

Our simulation experiments distinctly support the idea that using information about the environment (here population density) in dispersal decisions will usually increase the fitness expectations of individuals (Bowler and Benton, 2005; Clobert et al., 2009; Enfjäll and Leimar, 2009). Yet our results also demonstrate that this information must be processed in the 'right way' to come to an adequate dispersal decision. If this is not the case, an information-based strategy might even perform worse than a strategy, which simply ignores this piece of information: in our simulations the unconditional strategy DI with constant emigration probabilities outcompeted the 'informed' but inadequate threshold strategy T. This certainly is a message of more general validity. It is not sufficient to note that the use of information in behavioural decisions would be useful – this will only be true if the information is 'translated' into behavioural decisions according to an appropriate rule, i.e. a rule with the correct quantitative link between input (stimulus) and response. Considering our experiments it is thus not surprising, but assuring that the theoretically derived 'link-function' between population density and emigration probability (TA) out-competes the pragmatically justified strategies TL and S.

When performing simulation experiments, the theoretical foundations of the dispersal functions implemented may not always be of primary concern, especially, because the different functions can be made to look quite similar over a limited range of population densities. Thus, more practical considerations, like the ease of implementation, the speed of evolution, or the straightforward interpretation of evolving parameters may be of greater relevance when making a choice about which dispersal strategy to implement in a simulation study. However, also in this respect the single-parameter strategy TA has advantages over the more complex models, especially the three-parameter model (strategy S) of

Kun and Scheuring (2006). In the monoculture experiments it took at least twice as long (ca. 4000 vs. 2000 time steps) for Kun and Scheuring's strategy to reach an equilibrium distribution in trait frequencies. This may lead to complications or artefacts in simulations involving dynamic landscapes or habitat conditions where the dispersal strategies continuously need to adjust to new conditions. This difficulty could eventually be overcome by incorporating crossover in simulations with diploid organisms and sexual reproduction. However, we cannot see an added benefit in following such a complex simulation approach, in comparison to implementing the simpler strategy TA (T for the case of continuous population growth).

## 5. Conclusion

We strongly recommend the use of the dispersal model introduced by Ruxton and Rohani (1998) and Poethke and Hovestadt (2002) in simulation studies incorporating density-dependent emigration and a discrete population model of the type used here. On the one hand, this is mandated by its theoretical foundation, while the models by Travis et al. (1999) and Kun and Scheuring (2006) as well as some others were introduced based on pragmatic arguments or even as arbitrary decisions. On the other hand, strategy TA has the benefit that it only needs a single evolving trait, which can rapidly adapt to the (changing) settings implemented in a simulation experiment. Equilibrium will thus be achieved more quickly (saving computation time) and the interpretation of the evolving 'genetic' trait is straightforward. Further, the model also allows accounting for effects of habitat heterogeneity and modified mechanism of population regulation in its extended version (Poethke and Hovestadt, 2002).

Clearly, our analysis is limited to the fundamental assumptions we made concerning the type of population regulation and mating system. For species with continuous population growth, alternative mating systems, e.g. monogamy, or different social systems, different emigration rules might be more appropriate. We thus generally recommend carefully considering, which information would be relevant in taking emigration decisions and how the quantitative link between emigration probability and this information should look like – ideally, such rules should be derived from first principle.

## Acknowledgement

This project was supported by funds from the 'Deutsche Forschungsgemeinschaft' to TH and HJP (DFG PO244/4).

## References

- Bach, L.A., Ripa, J., Lundberg, P., 2007. On the evolution of conditional dispersal under environmental and demographic stochasticity. *Evol. Ecol. Res.* 9, 663–673.
- Bellows, T.S., 1981. The descriptive properties of some models for density dependence. *J. Anim. Ecol.* 50, 139–156.
- Bowler, D.E., Benton, T.G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.* 80, 205–225.
- Brachet, S., Olivieri, I., Godelle, B., Klein, E., Frascaria-Lacoste, N., Gouyon, P.H., 1999. Dispersal and metapopulation viability in a heterogeneous landscape. *J. Theor. Biol.* 198, 479–495.
- Bullock, J.M., Kenward, R.E., Hails, R.S. (Eds.), 2002. *Dispersal Ecology*. Blackwell Publishing, Oxford, 458 p.
- Cadotte, M.W., 2006. Dispersal and species diversity: a meta-analysis. *Am. Nat.* 167, 913–924.
- Charnov, E.L., 1976. Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* 9, 129–136.
- Clark, J.S., Silman, M., Kern, R., Macklin, E., HilleRisLambers, J., 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80, 1475–1494.
- Clobert, J., Danchin, E., Dhont, A.A., Nichols, J.D. (Eds.), 2001. *Dispersal*. Oxford University Press, Oxford, 452 p.
- Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S., Massot, M., 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* 12, 197–209.
- Conradt, L., Bodsorth, E.J., Roper, T.J., Thomas, C.D., 2000. Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. *Proc. Roy. Soc. Lond. B* 267, 1505–1510.
- Enfjäll, K., Leimar, O., 2005. Density-dependent dispersal in the Glanville fritillary, *Melitaea cinxia*. *Oikos* 108, 465–472.
- Enfjäll, K., Leimar, O., 2009. The evolution of dispersal—the importance of information about population density and habitat characteristics. *Oikos* 118, 291–299.
- Frank, K., Wissel, C., 1998. Spatial aspects of metapopulation survival—from model results to rules of thumb for landscape management. *Landsc. Ecol.* 13, 363–379.
- Getz, W.M., Saltz, D., 2008. A framework for generating and analyzing movement paths on ecological landscapes. *Proc. Natl. Acad. Sci.* 105, 19066–19071.
- Hanski, I., 1999. *Metapopulation Ecology*. Oxford University Press, New York, 313 p.
- Hassell, M.P., 1998. The regulation of populations by density-dependent processes. In: Dempster, J.P., McLean, I.F.G. (Eds.), *Insect Populations in Theory and in Practice*. Kluwer Academic Publishers, Dordrecht, pp. 29–51.
- Herzig, A.L., 1995. Effects of population-density on long-distance dispersal in the Goldenrod Beetle *Tritrhabda virgata*. *Ecology* 76, 2044–2054.
- Holt, R.D., Barfield, M., 2001. On the relationship between the ideal free distribution and the evolution of dispersal. In: Clobert, J., Danchin, E., Dhont, A.A., Nichols, J.D. (Eds.), *Dispersal*. Oxford University Press, Oxford, pp. 83–95.
- Holt, R.D., McPeck, M.A., 1996. Chaotic population dynamics favors the evolution of dispersal. *Am. Nat.* 148, 709–718.
- Holyoak, M., Leibold, M.A., Holt, R.D. (Eds.), 2005. *Metacommunities: Spatial Dynamics and Ecological Communities*. University of Chicago Press, Chicago, 513 p.
- Hovestadt, T., Poethke, H.J., 2006. The control of emigration and its consequences for the survival of populations. *Ecol. Model.* 190, 443–453.
- Johst, K., Brandl, R., 1997. The effect of dispersal on local population dynamics. *Ecol. Model.* 104, 87–101.
- Johst, K., Doebeli, M., Brandl, R., 1999. Evolution of complex dynamics in spatially structured populations. *Proc. Roy. Soc. Lond. B* 266, 1147–1154.
- Kindlmann, P., Aviron, S., Burel, F., Quin, A., 2004. Can the assumption of a non-random search improve our prediction of butterfly fluxes between resource patches? *Ecol. Entomol.* 29, 447–456.
- Kun, A., Scheuring, I., 2006. The evolution of density-dependent dispersal in a noisy spatial population model. *Oikos* 115, 308–320.
- Lemel, J.Y., Belichon, S., Clobert, J., Hochberg, M.E., 1997. The evolution of dispersal in a two-patch system: some consequences of differences between migrants and residents. *Evol. Ecol.* 11, 613–629.
- Levine, J.M., Murrell, D.J., 2003. The community-level consequences of seed dispersal patterns. *Ann. Rev. Ecol. Syst.* 34, 549–574.
- Matthysen, E., 2005. Density-dependent dispersal in birds and mammals. *Ecography* 28, 403–416.
- Maynard-Smith, J., Slatkin, M., 1973. Stability of predator–prey systems. *Ecology* 54, 384–391.
- McPeck, M.A., Holt, R.D., 1992. The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.* 140, 1010–1027.
- Metz, J.A.J., Gyllenberg, M., 2001. How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionarily stable dispersal strategies. *Proc. Roy. Soc. Lond. B* 268, 499–508.
- Morris, D.W., Diffendorfer, J.E., 2004. Reciprocating dispersal by habitat-selecting white-footed mice. *Oikos* 107, 549–558.
- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. *Proc. Natl. Acad. Sci.* 105, 19052–19059.
- Poethke, H.J., Hovestadt, T., 2002. Evolution of density- and patch-size-dependent dispersal rates. *Proc. Roy. Soc. Lond. B* 269, 637–645.
- Poethke, H.J., Hovestadt, T., Mitesser, O., 2003. Local extinction and the evolution of dispersal rates: causes and correlations. *Am. Nat.* 161, 631–640.
- Poethke, H.J., Pfennig, B., Hovestadt, T., 2007. The relative contributions of individual- and kin-selection in the evolution of density-dependent dispersal rates. *Evol. Ecol. Res.* 9, 41–50.
- R Development Core Team, 2007. *R: A Language and Environment for Statistical Computing Vers. 2.5.0*. R Foundation for Statistical Computing, Vienna.
- Ranta, E., Lundberg, P., Kaitala, V., 1999. Resource matching with limited knowledge. *Oikos* 86, 383–385.
- Ruxton, G.D., Rohani, P., 1998. Fitness-dependent dispersal in metapopulations and its consequences for persistence and synchrony. *J. Anim. Ecol.* 68, 530–539.
- Travis, J.M.J., 2001. The color of noise and the evolution of dispersal. *Ecol. Res.* 16, 157–163.
- Travis, J.M.J., Dytham, C., 1998. The evolution of dispersal in a metapopulation: a spatially explicit, individual-based model. *Proc. Roy. Soc. Lond. B* 265, 17–23.
- Travis, J.M.J., Murrell, D.J., Dytham, C., 1999. The evolution of density-dependent dispersal. *Proc. Roy. Soc. Lond. B* 266, 1837–1842.
- Zobel, M., Otsus, M., Runk, K., Liira, J., 2005. Can long-distance dispersal shape the local and regional species pool? *Folia Geobot.* 40, 35–44.