The evolution of density-dependent dispersal under limited information

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ABSTRACT

For an increasing number of species dispersal decisions have been shown to depend on local population density. This implies that organisms perceive – with sufficient accuracy – information about population density. However, research on the fitness value of such information, the adequate use of imprecise information, and how information use affects overall dispersal has only just started.

A critical issue in such research necessarily concerns the adequate rule linking an individual's population density estimate to its readiness to emigrate; a spectrum of such rules has been proposed in the past. We use three prevalent rules and one rule specifically derived for situations of incomplete information to demonstrate that the adequacy of each rule strongly depends on the accuracy of information about population density: Simple bang–bang (threshold) behavior performs best if information is highly inaccurate, whereas a saturating response function (dispersal propensity gradually increasing with population density) out-competes all other strategies when individuals can estimate density accurately. The decision rule as well as the precision of information significantly influence average emigration probabilities establishing in metapopulations. Our results show that use of inadequate rules in models of dispersal evolution may lead to false dispersal decisions. Based on this analysis we present a rule that allows approximating an adequate dispersal response at the population level even when individuals possess incomplete information about local density. We conclude that individuals should generally invest little into the acquisition of (accurate) information even if such acquisition is associated with only small costs.

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1. Introduction

Many metapopulation models assume that dispersal is a completely random event (e.g. Hanski, 1999). Dispersal decisions, however, have far reaching consequences for an individual's (inclusive) fitness. Thus, natural selection should favor individuals that use available information about the environment to adjust emigration decisions in a fitness enhancing way (Bowler and Benton, 2005; Getz and Saltz, 2008; Nathan, 2008; Clobert et al., 2009). For example individuals could respond to cues signaling elevated predation pressure (Poethke et al., 2010), poor habitat quality (Clarke et al., 1997), or increased number of competitors (Metz and Gyllenberg, 2001; Poethke and Hovestadt, 2002) and consequently decide to emigrate.

An obvious case of an adaptive dispersal strategy is emigration from sites with intense competition over critical resources, i.e. emigration from high-density populations. Recognizing the local population density would allow an individual to predict its fitness expectation provided that it would remain philopatric and contrast this expectation with that if it would emigrate (Metz and Gyllenberg, 2001; Poethke and Hovestadt, 2002). There is indeed considerable empirical evidence that population density does affect emigration (Herzig, 1995; Kindlmann et al., 2004; Morris et al., 2004; Matthysen, 2005; Conradt and Roper, 2006; Enfjäll and Leimar, 2009; Nowicki and Vrabec, 2011) and implementing density dependence has become common practice in models of dispersal evolution (e.g. Ruxton and Rohani, 1999; Travis et al., 1999; Poethke and Hovestadt, 2002; Kun and

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Scheuring, 2006) and population viability (Hovestadt and Poethke, 2006).

A critical issue when implementing density-dependence into models of animal dispersal or fitting an according statistical model to empirical data is the choice of the appropriate 'response function' or 'decision rule', i.e. the behavioral 'reaction norm' linking population density to emigration decisions. A number of such rules has been proposed, ranging from a simple threshold rule (stay if local population size is below a critical value and disperse as soon as it is above this critical value; e.g. Metz and Gyllenberg, 2001) over simple linear (e.g. Travis et al., 1999) and nonlinear (e.g. Ruxton and Rohani, 1999; Poethke and Hovestadt, 2002) to flexible nonlinear functions (Kun and Scheuring, 2006; Johst and Brandl, 1997). Some of these rules were chosen quite arbitrarily. To our knowledge only two have been derived from theoretical principles: For populations with overlapping generations and continuous dispersal Metz and Gyllenberg (2001) showed that a simple 'bang–bang response' is the evolutionarily stable dispersal strategy. For non-overlapping generations with brief dispersal seasons Ruxton and Rohani (1999) suggested a one-parameter nonlinear response function which was later formally derived on the basis of a marginal value kind of argument by Poethke and Hovestadt (2002). Comparing this rule in an evolutionary tournament with three other, frequently implemented rules for emigration decisions Hovestadt et al. (2010) showed that this function indeed out-competes all tested alternatives.

All the models cited above assume, however, that each individual has completely accurate information about local population density when taking its decision. Under realistic conditions this will rarely be the case: Particularly for the case of natal dispersal, emigration decisions may be taken at a moment when individuals presumably have had too little time and experience to gather robust information about resource availability or the number of (competing) conspecifics in their natal patch (but see discussion). Most likely, individuals will thus base their dispersal decisions on more or less imprecise estimates of local population density.

In a recent simulation study Bocedi et al. (2012) call attention to the problem of dispersal decisions that are based on incomplete information. Using individual-based simulations they analyzed the influence of incomplete information on the evolution of optimal response functions. However, as they restrict the spectrum of allowed density-dependent responses to a specific type of sigmoid shape and used local competition as a proxy for local density their results have to be interpreted with caution (for a critical discussion of their approach see Poethke et al., 2016).

We expect that information (in)accuracy should have an impact on emigration probability and the evolution of emigration decision rules, i.e. on the specific shape of the response function. In this manuscript we will introduce an extended version of the simple rule derived by Ruxton and Rohani (1999); Poethke and Hovestadt (2002) to account for the effects of inaccurate information. We will investigate the efficiency of this modified rule in comparison to three alternative response functions taken from the literature. More specifically we will (i) directly contrast the performance of different decision rules in an evolutionary contest, (ii) utilize the improved rule to analyze the effect of information precision on evolving emigration probabilities, and (iii) investigate the evolution of investment into information acquisition provided that such acquisition is associated with a certain fertility cost (fertility-information trade-off), i.e. we will assess the fitness value of information.

2. Methods

2.1. Decision rules for inaccurate information

For the case of accurate information the decision rule of Ruxton and Rohani (1999) is the optimal response to population density. This has been shown in an evolutionary tournament by Hovestadt et al. (2010) and is easily explained by a marginal value type of argument (Poethke and Hovestadt (2002)). But which decision rule(s) can cope best with the problem of information inaccuracy? We will approach this problem by carrying out an evolutionary tournament (sensu Axelrod, 1984; see also Hovestadt et al., 2010) to contrast the ability of different candidate rules to best account for this problem.

We will compare the performance of three rules of different complexity that have previously been implemented in models of density-dependent emigration. In addition, we will propose a version of the model by Ruxton and Rohani (1999) modified for coping with only partially accurate information. We will describe the four candidate rules in the following:

2.1.1. Asymptotic threshold function (T_A)

This decision rule was first suggested by Ruxton and Rohani (1999). It is theoretically founded on a marginal value kind of argument (Poethke and Hovestadt, 2002) as its specific properties assure homogenization of fitness expectations for philopatric and dispersing individuals born in the same natal patch (Poethke et al., 2007). Similar to the model of Metz and Gyllenberg (2001) that applies in situations where emigration occurs continuously in time, the rule assumes no emigration below a certain threshold C_T. The single model parameter C_T defines the dispersal threshold but also influences the increase in emigration probability (emigration propensity) with estimated local population density N_i^E in patch i:

$$d_{TA}\left(N_i^E\right) = \begin{cases} 0 & \text{for} & N_i^E < C_T \\ 1 - \dfrac{C_T}{N_i^E} & \text{for} & N_i^E > C_T \end{cases} \tag{1}$$

2.1.2. Linear threshold function (T_L)

Travis et al. (1999) suggested a two-parameter linear decision rule. Accordingly, no emigration occurs below a certain threshold population density C_T. Above this threshold emigration probability d increases linearly with slope s until it reaches the maximum value of $d = 1$:

$$d_{TL}N_i^E = \begin{cases} 0 & \text{for} & N_i^E < C_T \\ s\left(N_i^E - C_T\right) & \text{for} & C_T \leq N_i^E \leq \dfrac{1}{s} + C_T \\ 1 & \text{for} & N_i^E > \dfrac{1}{s} + C_T \end{cases} \tag{2}$$

2.1.3. Sigmoid function (S)

A more flexible decision rule was proposed by Kun and Scheuring (2006) and has already been applied in an analysis of density-dependent dispersal under incomplete information by Bocedi et al. (2012; but see discussion). This model is characterized by three parameters: the maximum emigration probability D_0 $0 \leq D_0 \leq 1$, the slope α, and the inflection point β: Emigration propensity d is calculated as:

$$d_S\left(N_i^E\right) = \frac{D_0}{1 + \exp\left(-\alpha\left(N_i^E - \beta\right)\right)} \tag{3}$$

2.1.4. The extended asymptotic threshold function (T_{AE})

With incomplete information about the actual density in a patch, individuals will tend to over − or underestimate true density. To

account for the 'blurring' effect of such misjudgments on dispersal decisions we propose a modification of the original T_A rule by introducing a second parameter $\gamma \in [0; 1]$.

$$d_{TAE}\left(N_i^E\right) = \begin{cases} 0 & \text{for} \quad N_i^E < C_T \\ 1 - \dfrac{C_T \cdot (1-\gamma)}{N_i^E - C_T \cdot \gamma} & \text{for} \quad N_i^E \geq C_T \end{cases} \qquad (4)$$

The additional parameter γ controls the steepness of the density response (see Fig. 1). Setting $\gamma = 0$ recovers the asymptotic threshold model T_A (equation (1); see Fig. 1, dashed line); with increasing γ the function becomes steeper and d_{TAE} could ultimately approach a simple step function (as in Metz and Gyllenberg, 2001) where emigration probability jumps from 0 to 1 if $N_i^E > C_T$.

2.2. Individual-based simulations of trait evolution

We implemented evolutionary tournaments in individual-based simulations to decide which of these four candidate rules is most successful in coping with the problem of information inaccuracy and will consequently out-compete other rules. We did so by following the same two-step approach already described by Hovestadt et al. (2010, see below).

In all simulations individuals are assumed to live in a metapopulation of 5000 habitat patches linked by global dispersal of individuals between patches. Local population dynamics in each patch is modeled according to the growth model of Beverton and Holt (1957). Accordingly, each individual gives birth to a number of offspring, which is drawn from a Poisson distribution with mean fertility λ. Density-dependent competition then acts on the survival probability $s_{i,t}$ in patch i at time t of newborn individuals:

$$s_{i,t} = \frac{1}{1 + a_{i,t} L_{i,t}} \quad \text{with} \quad a_{i,t} = \frac{\lambda - 1}{K_{i,t} \cdot \lambda} \qquad (5)$$

with $L_{i,t}$ being population size of (new born) immature offspring and $K_{i,t}$ denoting local carrying capacity for adults in year t (the corresponding capacity of immature offspring would be $K_{i,t} \cdot \lambda$). We assume temporally and spatially uncorrelated annual fluctuations in growth conditions, represented by variation in $K_{i,t}$ (see also Bocedi et al., 2012; and Poethke et al., 2016): We draw values for the local carrying capacities $K_{i,t}$ for each year and each patch from a log-normal distribution with mean $K = 25$ and standard deviation σ ($\sigma = 0.0$, 12.5, or 25.0).

Following density-dependent survival but before reproduction, individuals may disperse with probability d: This probability d is calculated based on an individual's estimate of local population density in patch i N_i^E and the response function applied by this individual (d_{TA}, d_{TL}, d_S, or d_{TAE}, see eqs. (1), (2), (3), and (4)). Reproduction is asexual, individuals are haploid and the type of response function applied and parameter values are directly stored in the genome.

We assume that the precision of density estimates can be scaled between 0 and 1 (see below) with $I = 0$ meaning no information and $I = 1$ perfect (absolutely accurate) information. Note, however, that even without perceiving any direct information about the actual density of competitors in a patch, individuals may have some general knowledge – by own experience or by the long-term "experience" of a lineage encoded in the genome – about a plausible range of densities occurring in the metapopulation: In (evolutionary) equilibrium, the true distribution of local population sizes N_i of patches will follow a certain probability distribution $\Phi_0(N)$ in space and time. Individuals may use this distribution as a Bayesian prior for estimates of local density (see e.g. Smith, 1991). It determines the distribution Φ_E of estimated densities when no further information is available. However, with increasing precision of information I the distribution Φ_E of individual density estimates N_i^E in patch
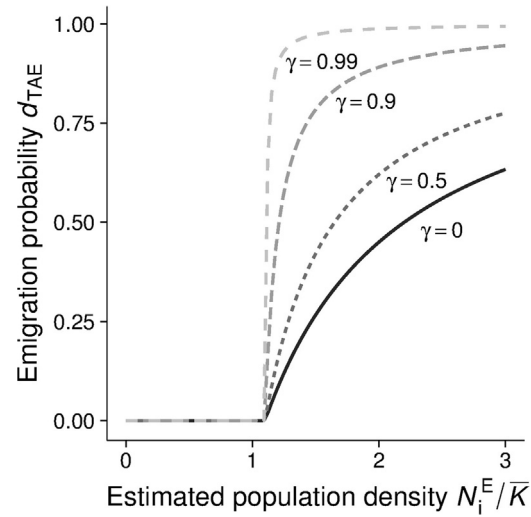

Fig. 1. Effect of scaling parameter γ of the T_{AE} decision rule (eq. (4)) for resulting emigration probability plotted over (normalized) estimated population density $N_i^E / \bar{K}$. For the case of complete information the T_{AE} rule can recover the asymptotic threshold model T_A (dashed line) by setting $\gamma = 0$. Parameter C_T is set to $C_T = 1.1 \cdot \bar{K}$.

i should increasingly approach the true density N_i. Ultimately, if completely accurate information ($I = 1$) about N_i is available, density estimates obviously must map the correct value, i.e. $N_i^E = N_i$ and the corresponding distribution Φ_E collapses into a Dirac delta-function $\delta(N_i)$ (Dirac, 1958). Such a Bayesian approach of density estimation based on limited information I may be formalized as:

$$\Phi_E \langle N_i^E | I, N_i, \Phi_0 \rangle = \frac{1}{1-I} \Phi_0 \left(\frac{N_i^E - I \cdot N_i}{1 - I} \right) \qquad (6)$$

Note that Φ_E integrates to 1 (integration by substitution) when $\Phi_0(N)$ integrates to 1. In analogy to this approach a density estimate for individual j of local population density in patch i at time-step t is generated as:

$$N_{i,j,t}^E = I \cdot N_{i,t} + (1-I) \cdot N_{RAN} \qquad (7)$$

with N_{RAN} a random number drawn from the equilibrium distribution Φ_0 of population sizes (for a formal proof of this approach see Hübner (2000), section 5.8)). We approximate Φ_0 by storing the population sizes N_i that occurred in the whole landscape during the last five generations. If no information is available to individuals ($I = 0$), $N_{i,j,t}^E = N_{RAN}$, whereas in the case of full information ($I = 1$) all individuals j correctly guess $N_{i,j,t}^E = N_{i,t}$.

Emigrants die before reaching their target patch with a probability $\mu = 0.1$; this mortality risk summarizes all potential fitness costs associated with dispersal (Bonte et al., 2012). In case of successful dispersal, immigrants are randomly assigned to one of the patches in the landscape (including the natal patch; 'global dispersal').

Offspring inherit the type of decision rule and all parameters associated with it from their parents; depending on the specific rule, individuals thus inherit either one (T_A), two (T_L, T_{AE}), or three parameters (S). Inherited parameter values may, however, mutate with probability m_t. In order to allow for sufficient genetic variation initially, and evolutionary fine tuning of the response functions later in the simulations, we let mutation probability m_t decline over simulation time according to

$$m_t = 0.01 \cdot e^{\left(\frac{-10 \cdot t}{t_{max}}\right)} \qquad (8)$$

with $t_{max} = 10{,}000$ generations the duration of simulations (see also Poethke and Hovestadt, 2002). If a mutation occurs, we add a random number drawn from a Gaussian distribution with mean

0 and standard deviation 0.2 to the inherited value of the corresponding allele.

2.3. Monoculture experiments

We first performed evolutionary simulations independently for each of the four candidate rules implemented in the population model described above and for each set of model parameters evaluated. For any candidate rule this allows identifying the parameter values that evolve in the absence of competition by individuals following other rules. Depending on the rule implemented individuals were initialized with the following values for the relevant parameters: (i) T_A: $C_T = 0.9 \cdot \bar{K}$, (ii) T_L: $C_T = 0.9 \cdot \bar{K}$, $s = 1$ (iii) T_{AE}: $C_T = 0.9 \cdot \bar{K}$, $\gamma = 0.0$ (iv) S: $D_0 = 1$, $< \alpha = 7$, $\beta = 1.5 \cdot K$.

Subsequently, the genomes (i.e. the inherited parameter values coded in the corresponding alleles) from the last generation of these experiments were stored to be used for initializing genomes of individuals in the following evolutionary tournament.

2.4. Evolutionary tournaments

The idea of the evolutionary tournament implies putting individuals that follow different decision rules into direct competition. More specifically, we conducted pairwise competition experiments, in which − at initialization − half of the individuals apply one of the four decision rules and the rest another competing strategy. For this purpose 50% of individuals were sampled from those stored at the end of the monoculture experiment for one decision rule and the remaining 50% of individuals from the monoculture experiment for another rule. Mutation probability m_t was set to zero in the tournaments. Simulations were terminated at the moment at which the frequency of one of the two strategies had increased to >=95% within the whole metapopulation (recorded as a 'win' for that strategy) or after 10,000 generations had passed (in which case the tournament was counted as a 'draw').

For each set of population parameters tested we performed tournaments between the 6 possible combinations of strategies T_A, T_L, S, and T_{AE}. Monoculture experiments and the associated evolutionary tournaments were carried out for mean habitat capacity K = 25, fertility $\lambda = 2$, and all combinations of values for habitat variability $\sigma \in \{0, 12.5, 25\}$ and information accuracy $I \in \{0, 0.2, 0.5, 0.8, 1.0\}$. For each parameter setting, each competition experiment was replicated 50 times.

2.5. The influence of information on dispersal propensity

For the extended threshold rule (T_{AE}) we used the monoculture simulations described above to further analyze the influence of information accuracy I on parameter evolution (C_T and γ) and emerging average emigration probabilities d. To collect corresponding data we continued the monoculture simulations for another 2000 generations (i.e. 12,000 generations in total). Over these 2000 generations (when evolutionary equilibrium was achieved) we sampled once every 100 generations the fraction of individuals that left their natal patch (mean emigration probability d) and the values of parameters C_T and γ of all individuals in the metapopulation. Means were calculated over all individuals included in these 20 samples. We repeated simulations with increasing levels of information accuracy ($I \in \{0, 0.05, 0.1 \ldots 1.0\}$). Note that for $I = 0$ completely density independent emigration must result as in this case individuals cannot adjust their emigration decision according to local density.

2.6. The fitness value of information

Using a modified version of the monoculture experiments we also investigated the evolution of investment into 'information acquisition' for the T_{AE} rule. To do so we introduced an additional heritable trait that determines the accuracy I_j of the density estimates of bearer j of this trait − in contrast to the simulations described before I is thus a freely evolving trait. To introduce costs related to information acquisition we linearly reduced the expected fertility of individual j in dependence of the chosen precision of density estimates I_j:

$$\lambda_j = \lambda \cdot \left(1 - \tau \cdot I_j\right) \quad \text{with} \quad 0 \leq \tau \leq 0.2 \qquad (9)$$

The simulation parameter τ thus determines the cost of information acquisition, i.e. the strength of the trade-off between investment into information acquisition I_j and fertility. At the start of any simulation experiment individuals were assigned random values for I_j drawn from a uniform distribution $I_j \in [0,1]$. This trait mutates with the same probability as the parameters determining dispersal behavior of individuals; mutants were generated as described before but values for I_j were restricted to the range [0,1].

We provide C++ code for simulations, simulation raw data, and R code (R Core Team, 2015) for generating figures on GitHub under https://github.com/akubisch/smart_disp.

3. Results

3.1. Monoculture experiments

The functions emerging after 10,000 steps in the monoculture experiments clearly demonstrate how the steepness of evolved individual responses to density declines as information accuracy (I) increases (Fig. 2). With larger environmental fluctuations individual threshold densities decline (i.e. individuals disperse already at lower densities). While the evolving shapes of decision rules differ substantially for low information accuracy ($I = 0.2$) and for low environmental fluctuations ($\sigma = 0$) they become more and more similar as environmental fluctuations and the accuracy of information increase.

3.2. Evolutionary tournaments

Across all values of σ tested in the evolutionary tournaments the modified threshold decision model T_{AE} out-competed rules T_L and S if information accuracy was large ($I = 0.8$); in these scenarios the original T_A rule performed more or less equally well as T_{AE} (Fig. 3). With lower values of I tested, results were less decisive, however. Rule T_{AE} kept its top rank in all competitions while rule T_L took second place in most competitions. The ranking of the simple T_A threshold model is clear: Always shared first if $I = 0.8$, always (shared) last otherwise.

3.3. The influence of information on dispersal propensity

Throughout the simulation experiments increasing the accuracy of information I about local population density resulted in a reduction of emigration probabilities d. This effect is more pronounced if environmental conditions become more variable: Under substantial environmental fluctuations ($\sigma = 25$) the difference in emigration probability between completely uninformed ($I = 0.0$) and fully informed individuals ($I = 1.0$) is larger than 30% (Fig. 4a).

The threshold density C_T shows only a weak evolutionary response to changes in information accuracy I (Fig. 4b) but a consistent decline as environmental variability σ increases. In contrast, the scaling parameter γ shows a strong and consistent evolution-
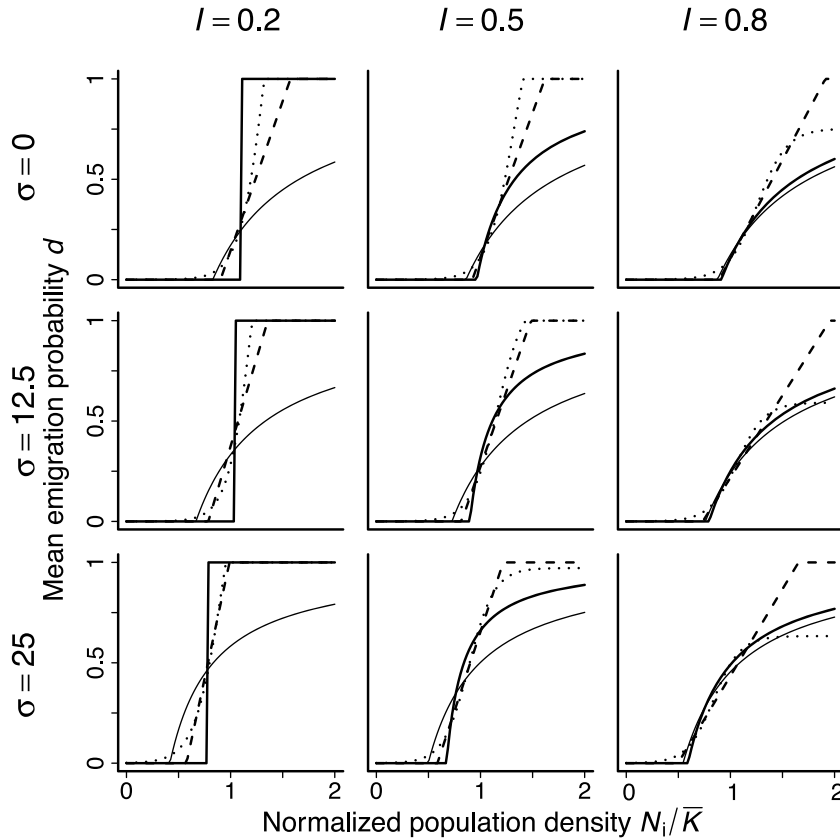
Fig. 2. Emergent mean shape of the different decision rules based on evolved mean parameter values for each rule in monoculture experiments (T_{AE}, bold continuous line; T_A narrow continuous line; T_L dashed line; S dotted line). Monoculture experiments were performed with constant mean carrying capacity K = 25, growth rate λ = 2, and dispersal mortality μ = 0.1. Across the nine panels we modulated the amount of environmental variability σ (strength of fluctuations of K), and the accuracy of information I on population density. Simulations ran over 10,000 generations.

ary response to changes in I_j (Fig. 4c): Larger values for γ evolve as I_j becomes smaller. Indeed, for values of I_j<0.4 a simple step-function with $\gamma\sim 1$ emerges (cf. Fig. 1). In turn, with completely accurate information (I_j = 1.0), a re-scaling of the 'original' decision rule T_A is no longer necessary. Consequently, γ evolves towards $\gamma = 0$ and the extended threshold function T_{AE} converges to T_A. It is worth noting that environmental variability σ severely influences emigration probability (and parameter C_T) but only has a minor impact on the evolution of the scaling parameter γ.

3.4. The fitness value of information

Under all scenarios tested investment into information accuracy evolves (more or less) to the maximum value I_j = 1 if this comes without any fertility cost (Fig. 5). However, it does obviously not pay to invest much into information acquisition; individuals invest only when the associated fertility cost is very low. Indeed, we find a unimodal relationship between the trade-off parameter τ (eq. (9)) and the absolute fertility cost evolving due to selection on I_j. As the trade-off parameter τ becomes too large the evolving values for I_j approach zero; as a consequence, density-independent emigration evolves under such circumstances. This holds for any of the four decision rules tested.

The amount of environmental variability σ has, however, a dominant effect on the evolution of I_j and consequently the investment into information acquisition. The larger σ, the larger the investment into information acquisition. The 'limit to investment' consequently increases from approx. $\tau \geq 0.03$ to approx. $\tau \geq 0.07$ as σ is increased from 0.0 to 25 (Fig. 5).

4. Discussion

It is interesting to note that – with high information accuracy (I = 0.8) and increasing levels of environmental fluctuations – the evolving shapes of all tested response functions become more and more similar and approach the shape of the theoretically derived T_A model (Fig. 2). This result may be explained by the fact that the evolutionary benefit associated with the "appropriate" use of information increases as inter-patch differences in density become larger and information becomes more precise. In this regard our results significantly differ from those given in Bocedi et al. (2012); see their Fig. 1. However, this discrepancy is most probably explained by the restriction they impose on the evolution of parameters and on their choice of proxy for density (for a detailed discussion see Poethke et al., 2016).

The original T_A model assures homogenization of fitness expectations for philopatric and dispersing individuals born in the same natal patch (Poethke et al., 2007) provided that density information is fully accurate. For situations of complete information the asymptotic response function (T_A) will thus necessarily perform better than any other decision rules (Hovestadt et al., 2010). In contrast to the sigmoid (S) or linear (T_L) strategies the extended response function (T_{AE}) can – with $\gamma \to 0$ – exactly recover the shape of the T_A function (see e.g. Fig. 2, σ = 25, I = 0.8). It is thus not surprising that it can also out-compete the linear (T_L) and sigmoid (S) response whenever information accuracy is high (e.g. I = 0.8).

The T_A strategy is – strictly speaking – applicable for situations of complete information availability (I = 1) only. In reality, any individual's density estimate will depend on e.g. a personal history of encounters with con-specifics, traces of their presence (cf. Bocedi
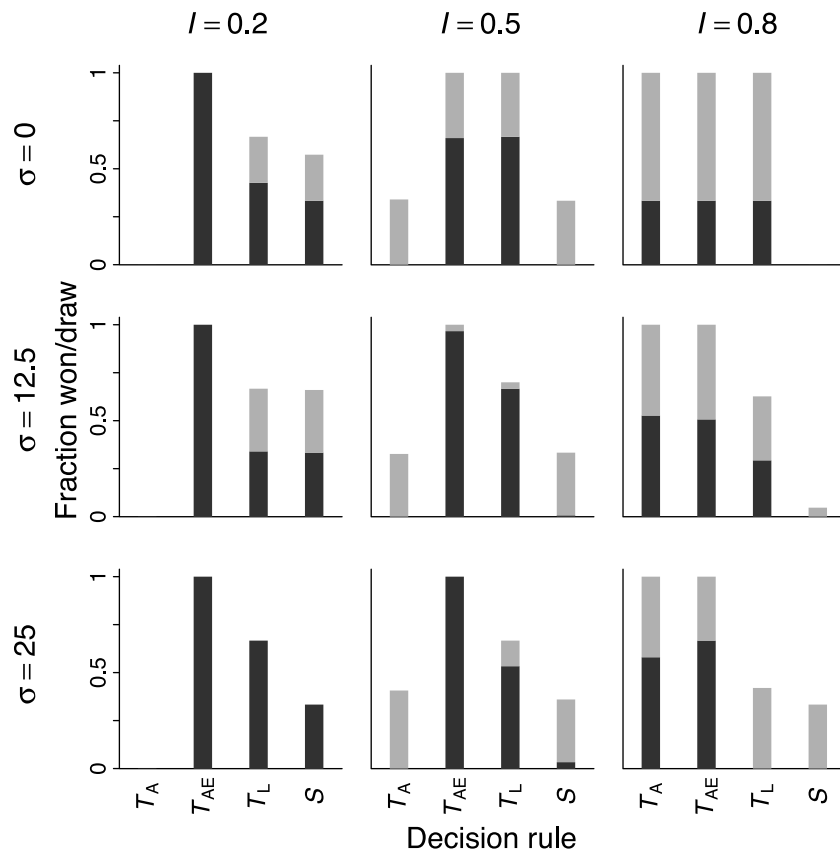
Fig. 3. Results of evolutionary tournaments between the four different decision rules T_A, T_{AE}, T_L, and S (see Methods for details). Figure is based on outcome of 50 replicate competitive tournaments for each possible combination of strategies. Proportion of contests won by a strategy is indicated by black coloration, proportion of draws by gray shading (see section Methods for details). In all contests mean carrying capacity K = 25 (parameter σ gives the standard deviation of fluctuations in K), growth rate λ = 2, and dispersal mortality μ = 0.1. Tournaments ran over 10,000 generations – simulations were initialized with 50% of individuals following either of the competing strategies. Initial genetic parameters were drawn from the set of individuals stored at the end of the corresponding monoculture experiments. A detailed tabulation of all pairwise tournaments is provided in Appendix A.

et al., 2012), or just on the availability of unexploited resources. As such histories are unique, density-estimates must vary among individuals within a population. Thus, whatever the individual decision rule, information inaccuracy will always have the consequence that this rule becomes 'blurred' at the population level. This blurring can, at least partially, be counteracted by an increased steepness of the decision rule used. This tendency of increased steepness with decreasing information can be observed for rules T_{AE}, T_L and S in the evolutionary tournaments.

Indeed, at low accuracy, i.e. at values of $I \leq 0.4$, the scale parameter of the winning strategy T_{AE} evolves towards $\gamma = 1$ (Fig. 2) resulting in the evolution of a simple step function. Due to its inflexibility (one evolvable parameter only) T_A simply cannot evolve into such a shape and consequently it performs poorly in the evolutionary contests in these scenarios. The T_L (two parameters) and S (three parameters) rules, however, could in principle also evolve into step functions and consequently could become more or less similar for the optimal T_L, S, and T_{AE} rules in the lower range of information accuracy (Fig. 2). Yet even in this range, T_{AE} out-competes the other rules in most tournaments, especially rule S (Fig. 3). This is particularly interesting as sigmoid response functions are rather frequently implemented in models of density dependent dispersal (e.g. Ives and Settle, 1997; Palmquist et al., 2000; Ylikarjula et al., 2000; Kun and Scheuring, 2006; Bocedi et al., 2012, 2014). The observed disadvantage of the sigmoid response function S presumably is a consequence of its inability to develop – for population densities just above threshold density – a concave down (increasing) shape (compare the shape of different decision rules

evolving in the monoculture experiment shown in Fig. 2). Additional simulation experiments with a slightly modified sigmoid function (allowing for a concave down shape in this range of density values) confirm this hypothesis (see Table A1 and Figs. A1 and A2 in the appendix). In individual-based evolutionary contests this disadvantage of the sigmoid response function is definitely amplified by the larger number of interacting strategy parameters that impairs evolutionary fine-tuning. The poorer performance of parameter rich decision models has already been discussed by Hovestadt et al. (2010). Nonetheless, as I approaches zero the shape of the response function becomes in fact irrelevant – whatever the shape of a decision rule – only density independent emigration can emerge.

The original marginal-value argument underlying the derivation of the original T_A model outlined in the original paper by (Poethke and Hovestadt (2002), see also Metz and Gyllenberg, 2001; Cressman and Křivan, 2006) is based on the idea that the principle of fitness homogenization and establishment of an ideal-free distribution are the underlying mechanisms driving the evolution of emigration rates. However, with inaccurate information individuals will tend to emigrate 'too early' or 'too late' compared to the ideal response due to misjudgments about the true population density. At the population level this will blur (and 'flatten') the relationship between population density and emigration response and undermine the establishment of an ideal-free distribution. The rational behind our modification of the T_A rule was that allowing for the evolution of a steeper response function could at least in part compensate for this effect. This proposed modification of the
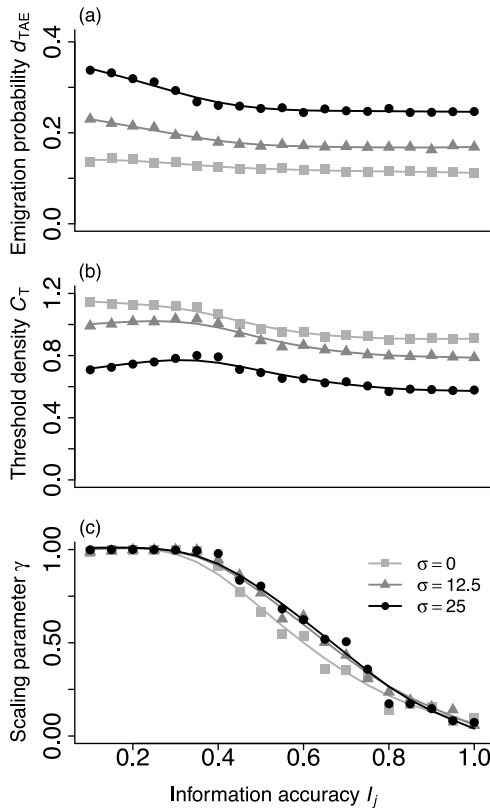
Fig. 4. Influence of information accuracy I_j on (a) the emergent mean emigration probability d_{TAE}, (b) the evolving threshold density C_T, and (c) the evolving scaling parameter γ for three different levels of environmental variability ($\sigma = 0$, light grey squares and line; $\sigma = 12.5$, dark grey triangles and line; $\sigma = 25$, black dots and line). Data shown are mean values evolving in a metapopulation of 5000 local populations after 10,000 generations. Carrying capacity of local populations K = 25, maximum rate of population increase $\lambda = 2$, dispersal mortality $\mu = 0.1$ in all simulations.

Fig. 5. Influence of the relative cost of information acquisition τ (eq. (9)) on (a) the actual amount of information acquired (I_j) and (b) the realized investment into information acquisition (measured by the reduction in fertility $\tau \cdot I_j$) for different levels of environmental variability σ. Each data point gives the mean values that evolved for a given combination of σ and τ after 10,000 generations. In all simulations decision rule was T_{AE}, mean carrying capacity of local populations was K = 25, maximum fertility $\lambda = 2$, and dispersal mortality $\mu = 0.1$.

original T_A rule is indeed more effective in dealing with information inaccuracy than some other conceivable rules. However, other than in the case of complete information (Poethke and Hovestadt, 2002; Hovestadt et al., 2014) we could not find an analytical solution to determine the optimal type of decision rule. We thus cannot exclude with complete certainty that other functional types for the decision rule could perform as well (or even better) than the proposed T_{AE} rule. This is a challenge to be solved in future studies.

It has previously been stated that informed emigration should generally result in lower emigration probabilities (Enfjäll and Leimar, 2009; Hovestadt et al., 2010; Poethke et al., 2011). Our results confirm this finding (Fig. 4). This is the case because informed (density-dependent) emigration is more effective in equalizing fitness expectations across a landscape: With more precise information about density in the local (and − if applicable − in the target patch) fewer dispersers are needed to approach an ideal free distribution of individuals (Cressman and Křivan, 2006). However, a particularly interesting result of our simulation experiments is the pronounced non-linear relationship between information accuracy and emigration probability: Only once information accuracy falls below a certain level (approximately $I < 0.4$) do we observe a noticeable increase in emigration probability. This may be traced to the differing effect of changes in information accuracy (I) on the evolutionary response of the two parameters (C_T and γ) of decision rule T_{AE} (see Fig. 4). As I declines we first observe a selective response only in the scaling parameter γ, while the threshold density C_T is hardly affected. Seemingly the scaling parameter allows to adequately compensate for the blurring of density information in this range. Only once information drops below
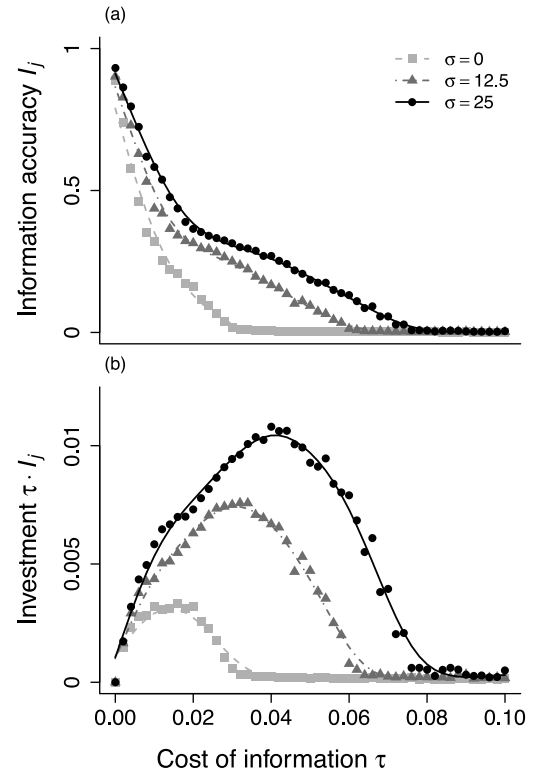
$I = 0.4$ and γ approaches its maximum value of one (turning the decision rule into a step-function) do we recognize a stronger evolutionary response in the threshold density C_T. It is this decrease of C_T that results in a noticeable increase in emigration probabilities whereas γ has as such little impact on mean emigration.

The simulations including a fertility-information trade-off demonstrate selection for higher investment into information acquisition as environmental stochasticity increases. This is a foreseeable result as under more variable environmental conditions variability in population densities across the landscape becomes larger, too. This in turn increases the potential for fitness improvement based on informed decision simply because emigration may result in a more substantial reduction from pre- to post-dispersal density for migrating individuals (Gros et al., 2009). Nonetheless, our simulation results seemingly indicate that the overall fitness benefit of informed emigration may be quite small. Indeed, in no scenario did selection result in a more than approximately 1% reduction in fertility in favor of information acquisition; beyond a certain threshold value for the slope of the trade-off function only completely uninformed emigration evolved.

We must be careful in interpreting the evolution of low investment into information acquisition, however. First, our result do not provide answers to the question what the fitness benefit of an informed mutant would be that emerges in a population of completely uninformed individuals (see also Olsson and Brown, 2010): The value of information for each individual necessarily declines with an increase in the number of informed individuals. Further, the population level response may already approximate the ideal response with good efficiency even if individuals are only moderately well informed. Second, and more importantly, it is not easy

to estimate how costly information acquisition in real life is. In the context of our model such costs should only be counted where they indeed involve an added investment. Yet, 'an individual's estimate of population density (or other attributes of patch quality) is presumably formed gradually over time based on e.g. the sequence (number, temporal distribution) of direct encounters with competitors (see e.g. Applebaum and Heifetz, 1999; Bauer et al., 2004) or more indirectly based on encounters with suitable or already exploited resources (indicating presence of competitors) like host plants (e.g. Van Gils, 2010). Indeed, density may even be 'deduced' just from the personal 'hunger level'. Such encounters, however, occur during regular foraging or egg laying movement anyway and may require little or no extra investment. Alternatively, information on population density (crowding) may have been collected already in a long larval phase. In other words, we have currently little knowledge to what extend animals move just for the sake of collecting information (see e.g. Bennetts and Kitchens, 2000; Van Dyck and Baguette, 2005; Conradt and Roper, 2006; McIntire et al., 2013). It is equally unclear to what degree investment into the sensory or cognitive 'apparatus' of animals can be attributed to the specific task of estimating population density (or patch quality): For an individual that has such cognitive abilities anyway, hardly any additional costs may be associated with using them also for the purpose of density estimation. At this moment we can only speculate that information will often become available almost free of cost but it is certainly a challenging task to identify how much animals do in fact invest into the acquisition of information. In this context we should also not forget that information about a habitat or home range is not just relevant for taking the decision to emigrate or not – familiarity with a certain region (which means possessing information about that area) carries great benefits in many circumstances (Brown et al., 2008) and may in itself be an important factor promoting philopatry.

It has already been pointed out by Bocedi et al. (2012) and emphasized by our results that under information inaccuracy the identity between population level response and individual decision rule disappears. This is an issue of empirical relevance and should have consequences for the way in which decision rules could be deduced from empirical data. Simple mass-marking approaches can provide information about the population level response. However, the identification of the underlying behavioral decision rule would require a more careful experimental approach exposing individuals to controlled conditions and keeping track of an individuals' history before it takes a decision.

In conclusion, the simulations presented here provide some theoretical insights concerning the effect and relevance of only partially reliable information for decision taking. It may be a useful message for theoreticians and modelers that a change in information accuracy will typically also have an effect on the best rule 'translating' information into decisions: Especially in rule-based modeling studies it is important to choose such decision rules wisely – taking a wrong choice may lead to misleading conclusions. For a specific but frequently utilized class of metapopulation models we here propose a sensible and simple rule for emigration decision taking to be implemented into such models.

Acknowledgements

Appendix A.

Table A1
Pairwise results of tournaments (see section Methods for further details and Figs. 3 and Fig. A1 for a graphical summary representation of these results).

| I	σ	pairing	draw	T_A	T_{AE}	L	S	S_M
0.2	0	L/TA	0	0	–	100	–	/
0.2	0	L/TAE	0	–	100	0	–	/
0.2	0	L/S	72	–	–	28	0	/
0.2	0	TA/TAE	0	0	100	–	–	/
0.2	0	TA/S	0	0	–	–	100	/
0.2	0	TAE/S	0	–	100	–	0	/
0.2	0	L/SM	92	–	–	8	/	0
0.2	0	TA/SM	0	0	–	–	/	100
0.2	0	TAE/SM	0	–	100	–	/	0
0.2	12.5	L/TA	0	0	–	100	–	/
0.2	12.5	L/TAE	0	–	100	0	–	/
0.2	12.5	L/S	98	–	–	2	0	/
0.2	12.5	TA/TAE	0	0	100	–	–	/
0.2	12.5	TA/S	0	0	–	–	100	/
0.2	12.5	TAE/S	0	–	100	–	0	/
0.2	12.5	L/SM	0	–	–	100	/	0
0.2	12.5	TA/SM	0	0	–	–	/	100
0.2	12.5	TAE/SM	0	–	100	–	/	0
0.2	25	L/TA	0	0	–	100	–	/
0.2	25	L/TAE	0	–	100	0	–	/
0.2	25	L/S	0	–	–	100	0	/
0.2	25	TA/TAE	0	0	100	–	–	/
0.2	25	TA/S	0	0	–	–	100	/
0.2	25	TAE/S	0	–	100	–	0	/
0.2	25	L/SM	0	–	–	100	/	0
0.2	25	TA/SM	0	0	–	–	/	100
0.2	25	TAE/SM	0	–	100	–	/	0
0.5	0	L/TA	0	0	–	100	–	/
0.5	0	L/TAE	100	–	0	0	–	/
0.5	0	L/S	0	–	–	100	0	/
0.5	0	TA/TAE	2	0	98	–	–	/
0.5	0	TA/S	100	0	–	–	0	/
0.5	0	TAE/S	0	–	100	–	0	/
0.5	0	L/SM	98	–	–	0	/	2
0.5	0	TA/SM	0	0	–	–	/	100
0.5	0	TAE/SM	100	–	0	–	/	0
0.5	12.5	L/TA	0	0	–	100	–	/
0.5	12.5	L/TAE	10	–	90	0	–	/
0.5	12.5	L/S	0	–	–	100	0	/
0.5	12.5	TA/TAE	0	0	100	–	–	/
0.5	12.5	TA/S	98	0	–	–	2	/
0.5	12.5	TAE/S	0	–	100	–	0	/
0.5	12.5	L/SM	68	–	–	0	/	32
0.5	12.5	TA/SM	0	0	–	–	/	100
0.5	12.5	TAE/SM	100	–	0	–	/	0
0.5	25	L/TA	32	0	–	68	–	/
0.5	25	L/TAE	0	–	100	0	–	/
0.5	25	L/S	8	–	–	92	0	/
0.5	25	TA/TAE	0	0	100	–	–	/
0.5	25	TA/S	90	0	–	–	10	/
0.5	25	TAE/S	0	–	100	–	0	/
0.5	25	L/SM	12	–	–	0	/	88
0.5	25	TA/SM	0	0	–	–	/	100
0.5	25	TAE/SM	70	–	30	–	/	0
0.8	0	L/TA	100	0	–	0	–	/
0.8	0	L/TAE	100	–	0	0	–	/
0.8	0	L/S	0	–	–	100	0	/
0.8	0	TA/TAE	100	0	0	–	–	/
0.8	0	TA/S	0	100	–	–	0	/
0.8	0	TAE/S	0	–	100	–	0	/
0.8	0	L/SM	100	–	–	0	/	0
0.8	0	TA/SM	100	0	–	–	/	0
0.8	0	TAE/SM	100	–	0	–	/	0
0.8	12.5	L/TA	40	60	–	0	–	/
0.8	12.5	L/TAE	48	–	52	0	–	/
0.8	12.5	L/S	12	–	–	88	0	/
0.8	12.5	TA/TAE	100	0	0	–	–	/
0.8	12.5	TA/S	2	98	–	–	0	/
0.8	12.5	TAE/S	0	–	100	–	0	/
0.8	12.5	L/SM	100	–	–	0	/	0
0.8	12.5	TA/SM	100	0	–	–	/	0
0.8	12.5	TAE/SM	100	–	0	–	/	0
0.8	25	L/TA	26	74	–	0	–	/
0.8	25	L/TAE	0	–	100	0	–	/
0.8	25	L/S	100	–	–	0	0	/
0.8	25	TA/TAE	100	0	0	–	–	/
0.8	25	TA/S	0	100	–	–	0	/
0.8	25	TAE/S	0	–	100	–	0	/
0.8	25	L/SM	12	–	–	0	/	88
0.8	25	TA/SM	98	0	–	–	/	2
0.8	25	TAE/SM	96	–	4	–	/	0
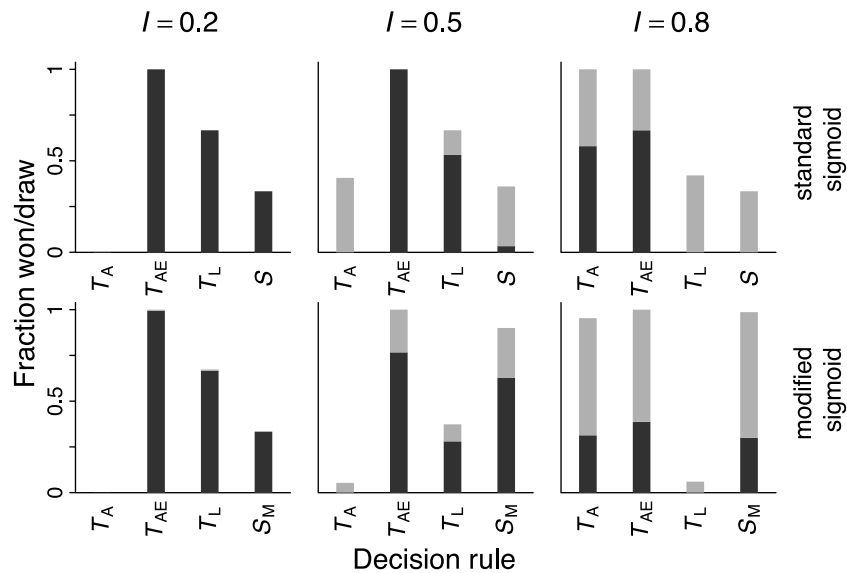
Fig. A1. Comparison of the performance of the standard sigmoid function (S, Equation 3) according to Kun and Scheuring (2006) with that of a modified version of the sigmoid function (S_M; $d_{SM}\left(N_i^E\right) = max\left[0,1/\left(1 + \exp\left(-\alpha\left(N_i^E - \beta r\right)\right)\right) - D_0\right]$) in tournaments between the four different decision rules (A) T_A, T_{AE}, T_L, S respective (B) T_A, T_{AE}, T_L, S_M. Proportion of contests won by a strategy is indicated by black coloration, proportion of draws by gray shading ($\sigma = 25$; see section Methods and Fig. 3 for further details). The modified sigmoid (S_M) performs better than the standard sigmoid (S) in situations of intermediate and high information.
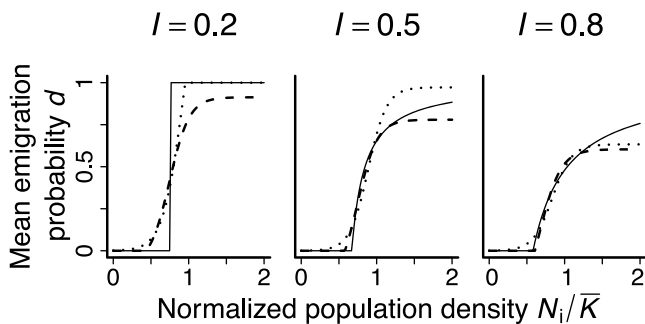

Fig. A2. Comparison of the emergent mean shape of the decision rules (T_{AE}, continuous line; S_M dashed line; S, dotted line) based on evolved parameter values for each rule in monoculture experiments . ($\sigma = 25$; initial values for strategy S_M: $D_0 = 0.0$, $\alpha\alpha = 7$, $\beta = 1.5 \cdot K$; see section Methods and Fig. 2 for further details). Clearly, the modified function (S_M) is better suited than function S to reproduce the critical upward concave shape of the model T_{AE}.

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