Comment

The Adequate Use of Limited Information in Dispersal Decisions

(A Comment on Bocedi et al., "Uncertainty and the Role of Information Acquisition in the Evolution of Context-Dependent Emigration")

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abstract: Several theoretical studies predict that informed (e.g., density-dependent) dispersal should generally result in lower emigration probabilities than uninformed (random) dispersal. In a 2012 publication, Bocedi et al. surprisingly come to the opposite conclusion. For most scenarios investigated, they found that noninformed and, particularly, less precisely informed dispersers evolve lower dispersal propensity than dispersers following "fully informed" strategies. Further, they observed that fully informed individuals evolved a steplike dispersal response—a response to local density that contradicts theoretical predictions for organisms with nonoverlapping generations. Replicating the individual-based simulations of Bocedi et al. we find that these conclusions are not justified and are based on a misinterpretation of simulation results: their controversial findings result from (i) a misleading use of the term "population density," (ii) a misconception concerning the true informative value of the different decision criteria they compared, and (iii) arbitrary constraints on the evolution of the dispersal response that prevented the evolution of strategies that allow for a fitness-enhancing utilization of available information.

Keywords: decision rule, dispersal, information processing, evolutionary tournament.

Introduction

A number of theoretical studies have come to the conclusion that taking informed emigration decisions into account should generally result in lower emigration probabilities (Enfjäll and Leimar 2009; Hovestadt et al. 2010; Poethke et al. 2011) than constant dispersal (random emigration with constant dispersal probability). This predic-

tion is readily explained by the fact that density-dependent emigration is more effective at equalizing fitness expectations across landscapes: with more precise information about density in the local (and, if applicable, in the target) patch, less dispersers are needed to approach an ideal free distribution of individuals (Cressman and Křivan 2006; Poethke et al. 2011). It is thus unexpected and interesting that a recent simulation study by Bocedi et al. (2012) comes to an opposite conclusion (see their fig. 3). For most scenarios investigated, they find that "noninformed" dispersers evolve lower dispersal propensity than "fully informed" dispersers. Further, they observed that individuals that correctly estimate local population densities evolve a steplike dispersal response to population density (their fig. 1A). The evolution of such a response to local density in a discrete population model contradicts the findings of Travis et al. (1999) and the theoretical derivation of Poethke and Hovestadt (2002).

In the following, we will replicate (with some modifications) the individual-based simulations of Bocedi et al. and demonstrate that their controversial findings possibly result from (i) a misleading use of the term "population density," (ii) a misconception concerning the true informative value of different decision criteria used, and (iii) arbitrary constraints imposed on the evolution of the dispersal function in their simulations that prevent, for some of their simulation scenarios, the evolution of an adequate dispersal response. We will explain the consequences of these shortcomings and present individual-based simulations that confirm previous findings and theoretical expectations.

Bocedi et al. performed simulations for a broad spectrum of temporal correlations of habitat quality, ranging

from temporally constant differences in habitat quality to uncorrelated temporal fluctuations. We will restrict this comment to only the two extremes of this spectrum, with a clear focus on the latter case (uncorrelated temporal fluctuations of habitat quality).

Simulation Experiments on Informed versus Noninformed Dispersal in Fluctuating Environments

Bocedi et al. assume, as in previous studies (see, e.g., Travis et al. 1999; Poethke and Hovestadt 2002; Kun and Scheuring 2006), that an individual's emigration decision depends on its estimate of local population density (but see below for adequacy of this term) $C_{i,t}^e$ of patch i at time t. To calculate, based on this information, an emigration probability d, they implement the sigmoid decision rule originally proposed by Kun and Scheuring (2006):

$$d(C_{i,t}^e) = \frac{D_0}{1 + \exp(-\alpha(C_{i,t}^e - \beta))}. \quad (1)$$

Here, D_0 defines the maximum emigration probability, α the slope, and β the inflection point of the sigmoid response function. Contrary to Kun and Scheuring (2006), who utilized estimates of local population size $N_{i,t}^e$, that is, $C_{i,t}^e = N_{i,t}^e$ (see also Travis et al. 1999; Enfjäll and Leimar 2009), Bocedi et al. calculate estimates of local population density defined as $C_{i,t}^e = N_{i,t}^e/K_{i,t}$, that is, they relate population size to the current local habitat capacity $K_{i,t}$. As we will explain in more detail later, we argue that this quantity $N_{i,t}^e/K_{i,t}$ is more adequately taken as a measure of current local (resource) competition. In the following, we will use individual-based simulation experiments to analyze the influence of this particular type of information on the evolving optimum dispersal decisions and contrast it with outcomes if other decision criteria are used. In general, we follow the modeling approach of Bocedi et al. to allow comparison of results but deviate in some assumptions.

Difference 1. In order to increase dispersal rates and get more pronounced effects, we assumed a slightly higher fertility than Bocedi et al.

Difference 2. In order to prevent artifacts resulting from the mutation procedure, we used temporally decreasing mutation rates (simulated annealing) instead of fixed rates.

Difference 3. We generate mutations as modifications of the parental traits and not, as Bocedi et al. did, by drawing mutant traits from a fixed range.

Difference 4. Values for habitat quality are drawn from a log-normal (instead of normal) distribution.

Difference 5. For "noninformed" dispersal, we generate random estimates of population sizes that are not correlated to the true population size.

Difference 6. We implement global dispersal instead of nearest-neighbor dispersal.

In the appendix, available online, we provide arguments for choosing these modifications and explore to what extent these modifications affect our results.

The Model

We performed simulation experiments using a discrete generation metapopulation model according to four different decision scenarios. Just as Bocedi et al. did, we first assume that individuals use information on local population size $N_{i,t}$ and local habitat capacity $K_{i,t}$ in their dispersal decision ($C_{i,t}^e = N_{i,t}^e/K_{i,t}$). Individuals either know the local population size $N_{i,t}$ and capacity $K_{i,t}$ exactly ($C_{i,t}^e = N_{i,t}/K_{i,t}$; hereafter, scenario NK, equivalent to the "fully informed" case in Bocedi et al.) or else individuals randomly guess population size ($N_{i,t}^e = N_{ran}$, i.e., $C_{i,t}^e = N_{ran}/K_{i,t}$; hereafter, scenario RK). For this latter scenario, we randomly draw values for N_{ran} from the distribution of population sizes that established across the landscape during the last five generations. This restricts the spectrum of N_{ran} to plausible values and reflects the assumption that species have an evolutionarily acquired expectation of such distributions. For comparison with Bocedi and colleagues' scenario of less-informed dispersal (scenario λ1 in Bocedi et al., fig. 3*D*), we additionally present simulation studies with N_{ran} randomly drawn from a negative binomial distribution with a mean equal to $N_{i,t}$ in the appendix (see fig. A1*E*, available online).

In a second set of simulation experiments, we follow the approach of Enfjäll and Leimar (2009) and assume that individuals base dispersal decisions solely on estimates of local density ($C_{i,t}^e = N_{i,t}^e$). For this approach, we also performed simulations with informed ($N_{i,t}^e = N_{i,t}$; scenario N) and uninformed ($N_{i,t}^e = N_{ran}$; scenario R) individuals. As a reference scenario, we also performed simulations on the evolution of constant emigration probability, that is, individuals use no information at all—neither information on population size (as in scenarios NK and N) nor information on local habitat quality (as in scenarios RK and NK)—but emigrate with a (genetically determined) probability d independent of any estimator $C_{i,t}^e$ (scenario NO).

In all simulations, the landscape is composed of 5,000 patches of suitable habitat linked by random global dispersal (randomly chosen target patch) of individuals. Local population dynamics in each patch is modeled according to the growth model of Beverton and Holt (1957): each individual gives birth to a number of offspring, randomly drawn from a Poisson distribution with mean fertility $r = 2$ (for the influence of r on dispersal rates, see fig. A1*A* in the appendix). Density-dependent competition then acts on the survival probability $s_{i,t}$ of newborn individuals:

$$s_{i,t} = \frac{1}{1 + a_{i,t}N_{i,t}}$$

$$\text{with } a_{i,t} = \frac{r-1}{K_{i,t}}. \qquad (2)$$

$N_{i,t}$ is the population size in patch i, and $K_{i,t}$ is the patch's local carrying capacity at time t. We assume temporally and spatially uncorrelated annual fluctuations in patch capacity $K_{i,t}$ (similar to "white noise" scenarios in Bocedi et al.): we draw values for $K_{i,t}$ for each year and each patch from a log-normal distribution with $K_{mean} = 25$ and standard deviation $\sigma = 25.0$. Additional simulations with normally distributed values of $K_{i,t}$ are presented in the appendix (see fig. A1D).

Following density-dependent survival but before reproduction, individuals may emigrate with a probability d calculated for each individual according to equation (1) and based on the individuals' estimator $C_{i,t}^e$, on the one hand, and its inherited dispersal parameters (D_0, α, and β), on the other; in scenario NO, the single inherited parameter is simply the emigration probability d. Emigrants may die during dispersal, with a probability $\mu = 0.1$ that accounts for all potential fitness costs associated with dispersal (Bonte et al. 2012). Successful migrants are randomly assigned to one of the 5,000 habitat patches in the landscape (global dispersal). The influence of nearest-neighbor dispersal, as used by Bocedi et al., is analyzed in the appendix (see fig. A1F).

Reproduction is asexual. Offspring inherit all parameters determining their emigration response from their parents. Parameter values may, however, mutate with probability m_t. In order to allow for broad initial genetic variation but selective fine-tuning of decision rules later in the simulations, we let m_t decline over time according to $m_t = 0.01 \cdot \exp(-10 \cdot t/t_{max})$, with $t_{max} = 5,000$ (i.e., m_t declines from 0.01 to 4.5×10^{-7} over the course of a simulation run; see also Poethke and Hovestadt 2002). Additional simulations with constant mutation rate are found in the appendix (see fig. A1B). For data collection, we continue the simulation for another 2,000 generations, recording overall dispersal as well as dispersal-related parameters of all individuals once every 100 generations. In case of a mutation event, we modify the value of the corresponding parental allele (D_0, α, and β, or d in the case of constant dispersal NO) by adding a random number drawn from uniform distributions: for β, D_0, and d from the interval $[-0.2, +0.2]$ and for α from $[-1, +1]$. For the first generation, parameter values are drawn from the distributions $[-0.5 \leq \beta < 0.5]$, $[-5 \leq \alpha < +5]$, $[0.5 \leq D_0 < 1.5]$, and $[0 \leq d < 1]$, respectively. To analyze the influence of the mutation procedure on resulting dispersal rates, we also performed simulations with mutations (similarly to Bocedi et al.) randomly drawn

from the predefined ranges $0.0 \leq D_0 \leq 1.0$, $0.0 \leq \beta \leq 5.0$, and $0.0 \leq \alpha \leq 100.0$ (see fig. A1C).

Results

Our results demonstrate the significant influence of the type of information that might be available to individuals and the rules of using such information for taking emigration decisions (fig. 1)—in this respect, we analyze here more alternatives than Bocedi et al. Dispersers that base their decision on random guesses of population size only ($C_{i,t}^e = N_{ran}$; scenario R) evolve emigration probabilities identical to those of individuals that follow a genetically fixed rule (scenario NO); their mean emigration is higher than for populations of individuals utilizing accurate estimates of population size ($C_{i,t}^e = N_{i,t}^e$; scenario N). In contrast, individuals that randomly guess population size and utilize information on local habitat capacity only ($C_{i,t}^e = N_{ran}/K_{i,t}$; scenario RK) evolve lower emigration than those utilizing accurate estimates of local population size and habitat capacity ($C_{i,t}^e = N_{i,t}/K_{i,t}$; scenario NK); this finding agrees with
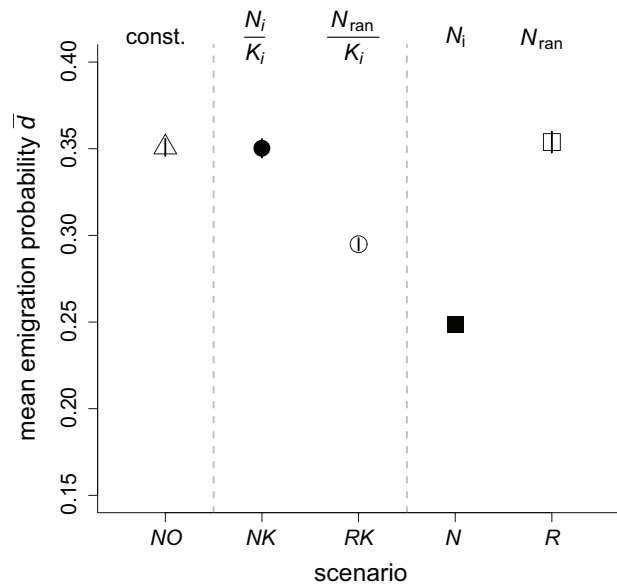

Figure 1: Influence of information use on evolved dispersal rates. NO = constant dispersal, NK = dispersal based on current population size and local habitat capacity ($C_{i,t}^e = N_{i,t}/K_{i,t}$), RK = dispersal based on habitat capacity (and random guess of population size; $C_{i,t}^e = N_{ran}/K_{i,t}$), N = dispersal based on population size ($C_{i,t}^e = N_{i,t}$), R = dispersal based on random guess of population size only (i.e., no information at all; $C_{i,t}^e = N_{ran}$). Circles represent scenarios with information on local habitat capacity $K_{i,t}$, and the triangle (constant dispersal) and rectangles represent scenarios without. Open symbols represent scenarios without information on population size $N_{i,t}$, and full symbols represent scenarios with exact information. For details regarding the different scenarios, see text.

that of Bocedi et al. However, as we will explain in the discussion, it does not support the authors' assertion that higher dispersal rates evolve in more fully informed individuals.

The evolved response functions for each scenario shown in figure 2 reveal two further insights. First, use of accurate estimates of local population size and local habitat capacity ($C_{i,t}^{e} = N_{i,t}/K_{i,t}$) results in evolution of a negative emigration response; that is, emigration probabilities decrease with increasing $C_{i,t}^{e}$ (fig. 2A), while the use of population size alone ($C_{i,t}^{e} = N_{i,t}$) leads to a positive response (fig. 2B). The second interesting result is the evolving steepness of response curves. If emigration decisions are based on random estimates of local population size only ($C_{i,t}^{e} = N_{\mathrm{ran}}$; scenario R), density estimates have, in fact, no influence on emigration (dashed line in fig. 2B). This is an expected and trivial finding, as these estimates contain no information about future conditions, and the evolving mean emigration probability is consequently similar to that evolving in scenario NO (genetically fixed emigration probability). In contrast, utilizing fully accurate information on $N_{i,t}$ results in a steep response function (compare scenarios N and R in fig. 2B). In contrast, if emigration decisions are based on local habitat quality only ($C_{i,t}^{e} = N_{\mathrm{ran}}/K_{i,t}$), the resulting response is significantly steeper than for the case where decisions are based on accurate estimates of population size and habitat quality ($C_{i,t}^{e} = N_{i,t}/K_{i,t}$; fig. 2A).

Discussion

Our results clearly contrast with those presented by Bocedi et al. First, we find that in spatiotemporally variable environments, increased information on local population density will result in the evolution of lower dispersal rates. Second, with full information on local population density, individual emigration propensity will not show a steplike response to density but nonlinearly increase with increasing density. The controversial findings of Bocedi et al. are—as we will outline in detail below—the consequence of misleading definitions used (mainly for the term "population density"), of misconceptions on the side of the authors about the informative value of the different density estimators used, and of undue restrictions in the evolution of response functions they implemented.

Under the model assumptions used here and by Bocedi et al. (i.e., natal dispersal, nonoverlapping generations), adults have to consider the effect of their emigration decision on the fitness (expectation) of their offspring, that is, the severity of competition their offspring are likely to face in the next generation. Depending on the strength of density dependence in survival and reproduction, population size ($N_{i,t}$) in this generation may indeed be a good estimator of future competition, and emigration decisions may thus sensibly be based on estimates of local population size ($N_{i,t}$) or density ($C_{i,t} = N_{i,t}/A_i$, population size per patch area A_i). All previous studies (see the introduction) have concluded that population-wide emigration probability should be lower if individuals utilize such information compared to populations where this is not the case. Bocedi et al., however, concluded just the opposite. We argue that this may be caused by a certain confusion concerning the definitions of population density used, especially in the theoretical literature.

Habitat capacity $K_{i,t}$, as a parameter used, for example, in models of population growth, depends itself on habitat
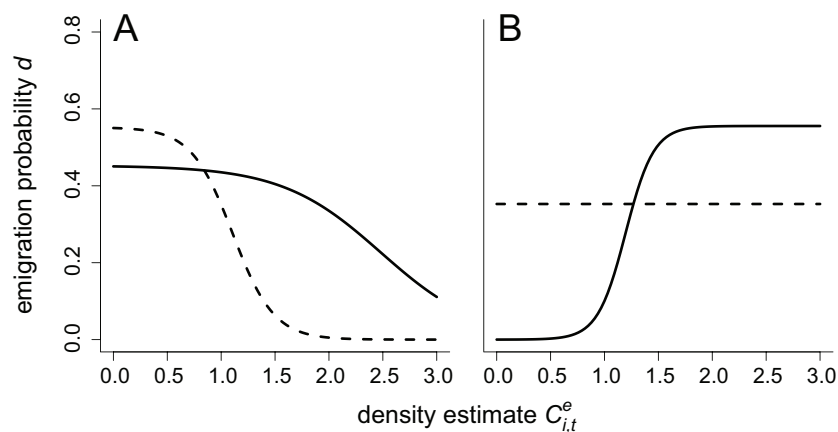

Figure 2: Influence of the use of information on evolved response functions. *A,* Individuals use information on local habitat quality $K_{i,t}$ and population size $N_{i,t}$ ($C_{i,t}^{e} = N_{i,t}/K_{i,t}$; scenario NK; solid line) or on local habitat quality and random estimates of population size ($C_{i,t}^{e} = N_{\mathrm{ran}}/K_{i,t}$; scenario RK; dashed line). *B,* Individuals use information on local population size $N_{i,t}$ (for better comparison with *A,* population size is normalized with mean capacity $\overline{K}$; i.e., $C_{i,t}^{e} = N_{i,t}/\overline{K}$; scenario N; solid line) or random estimates of population size only ($C_{i,t}^{e} = N_{\mathrm{ran}}/\overline{K}$; scenario R; dashed line). For details regarding the different scenarios, see text.

quality $Q_{i,t}$ and patch area A_i. Usually, empiricists define population density as $C_{i,t} = N_{i,t}/A_i$. However, in the modeling literature and particularly in models of density-dependent dispersal, it has become the general rule to define density as either $C_{i,t} = N_{i,t}$ (see, e.g., Kun and Scheuring 2006; Enfjäll and Leimar 2009) or $C_{i,t} = N_{i,t}/K_{i,t}$ (see, e.g., Travis et al. 1999; Poethke et al. 2002). The latter definition is not problematic as long as local habitat quality is assumed to be temporally constant, that is, $K_{i,t} = K_i$ = constant. However, in the model implementation of Bocedi et al. and of us in this comment (scenarios NK and RK), $K_{i,t}$ denotes a temporally fluctuating capacity (for a recent example, see Rodrigues and Johnstone 2014). These fluctuations may be driven by fluctuations in quality of patches (or a rather implausible fluctuation of habitat size), for example, due to year-to-year variability in resource availability. In this case, however, the estimator $C_{i,t}^e = N_{i,t}/K_{i,t}$ should, in our opinion, better be interpreted as a measure of (resource) competition in the parent generation (i.e., available resources per individual). Yet in the case of nonoverlapping generations, competition in the parent generation is not necessarily positively correlated with that in the offspring generation. In fact, provided that habitat quality $K_{i,t}$ shows temporally uncorrelated fluctuations (the white noise scenario in Bocedi et al.), it will typically be negatively correlated: low patch quality in the parent generation will result in low numbers of surviving offspring. As a consequence—and because, on average, poor years ($K_{i,t} < K_{mean}$) are followed by better years— low patch quality (strong resource competition) actually indicates weaker competition for the offspring that stay, that is, the parents of the next generation (for a very similar, seemingly counterintuitive effect of predation pressure on dispersal, see Poethke et al. 2010). Such a negative correlation must obviously select for a negative relation between local competition ($C_{i,t}^e = N_{i,t}/K_{i,t}$) experienced by parents and their emigration tendency (i.e., select for $\alpha < 0$), as we have indeed demonstrated (fig. 2A).

Unfortunately, Bocedi et al. restricted parameter evolution to predefined ranges (i.e., $0.0 \leq D_0 \leq 1.0$, $0.0 \leq \beta \leq 5.0$, and $0.0 \leq \alpha \leq 100.0$), thus allowing only for the evolution of positive competition dependence ($\alpha \geq 0$; see also our additional simulations in the appendix, fig. A1C). Further, they implemented a mutation rule that biases parameter values toward the center of the predefined range ("in the event of a mutation, the parameter assumed a new value randomly sampled from the same uniform distributions used to initialize the population" [Bocedi et al., p. 608]); most importantly, the evolution of the slope parameter α is thus biased toward $\alpha = 50$. Such a mutation algorithm may not be problematic if selection is strong and mutations are rare, but with three interacting parameters, selection is relatively weak (see Hovestadt et al. 2010), while the mutation rate used by Bocedi et al. is relatively high ($m = 0.001$). We as-

sume that this mutation algorithm, in concert with low selective pressure on each of the three interacting parameters of the rule, explains the evolution of steplike positive response functions reported by Bocedi et al. where a gradual negative response should have evolved (cf. fig. 2).

It is interesting that the individuals using accurate information on both local habitat quality and local population size (i.e., $C_{i,t}^e = N_{i,t}/K_{i,t}$; scenario NK) that were termed "informed" in the terminology of Bocedi et al. evolve emigration probabilities similar to those not using any information (scenarios NO and R). This suggests that local competition $C_{i,t}^e = N_{i,t}/K_{i,t}$ might, in fact, be less informative for emigration decisions than estimates of local habitat quality alone ($C_{i,t}^e = N_{ran}/K_{i,t}$). This hypothesis is supported by the significantly steeper slope in the response function that evolved when individuals use only information on local habitat quality ($C_{i,t}^e = N_{ran}/K_{i,t}$; fig. 2A) and validated by the Spearman's rank correlations (ρ) between future fitness in a patch ($F = r \cdot s_{i,t+1}$) and the various estimators utilized in the emigration decision: Current competition ($N_{i,t}/K_{i,t}$) correlates only very weakly with future fitness ($\rho = 0.056$), whereas $N_{ran}/K_{i,t}$ shows a substantially higher correlation of $\rho = 0.201$. However, the most reliable predictor of future conditions is population size ($N_{i,t}, \rho = -0.346$; all correlation coefficients were calculated for the constant dispersal scenario NO). Further, it is interesting to note that the estimator $1/K_{i,t}$ correlates better ($\rho = 0.250$) with future fitness than $N_{ran}/K_{i,t}$. This is not surprising, as including an additional random term in the estimator just obscures the accurate information on local habitat capacity. Contrary to what is assumed by Bocedi et al., accurately measuring present resource competition ($N_{i,t}/K_{i,t}$) in fact provides a very unreliable (uniformed) predictor of the future—our results here and even those of Bocedi et al. thus confirm and do not contradict (as claimed by Bocedi and colleagues) the previous findings that more informed individuals should generally disperse less.

The argumentation above changes under the assumption that local habitat quality $K_{i,t}$ is temporally correlated ("red noise" scenarios in Bocedi et al.) or even constant in time. In the latter case, the estimator $N_{i,t}^e/K_i$ will be a more reliable predictor of future competition, and the expectation of a positive correlation between local competition and optimal emigration is adequate: with persistent spatial heterogeneity in patch capacity, future competition in a patch is not only determined by actual population size but also by the proportional impact of immigrants on future competition. Under purely random immigration (as assumed by Bocedi et al. and us), this impact will be strongest for patches of low K_i. We have previously derived (Poethke and Hovestadt 2002) that optimal dispersal decisions should, in this case, ideally be based on separate estimates of local competition ($N_{i,t}^e/K_{i,t}$) and local habitat quality ($K_{i,t}$). The

relative strength of stochastic fluctuations (due to demographic or environmental effects) in population size compared to the spatial variance in habitat quality then determines which of these two estimates is more relevant for an adequate dispersal decision.

However, the decision rule used by Bocedi et al. (their eq. [1]) does not allow for a separate use of information about habitat quality and competition. Yet varying the precision of estimates of local competition $N_{i,t}^e/K_{i,t}$ shifts the balance between the contribution of competition and habitat quality on dispersal decisions. With very inaccurate or even totally random guesses of population size ($N_{i,t}^e = N_{\mathrm{ran}}$), dispersal decisions are primarily influenced by the estimate of patch capacity ($C_{i,t}^e = N_{\mathrm{ran}}/K_{i,t}$); by increasing the precision of $N_{i,t}^e$, the balance shifts in favor of competition-based emigration. This effect presumably explains why Bocedi et al. observed that individuals invest less into acquisition of information on local density (in their simulations, this investment is an evolving trait) in temporally constant than in moderately variable (red noise) environments (cf. panels *A* and *B* in their fig. 4): with large variance in habitat capacity, it is more relevant to know habitat capacity $K_{i,t}$ than available resources per individual $N_{i,t}/K_{i,t}$ for making sensible emigration decisions.

What is the most valuable information for dispersal decisions clearly depends on the temporal dynamics of environmental conditions. We have shown that in the case of fluctuations in habitat capacity, knowing local competition $N_{i,t}/K_{i,t}$ is not necessarily of great benefit due to the limited information content of this measure. In this case, either the size of the local population $N_{i,t}$ or both size $N_{i,t}$ and capacity $K_{i,t}$ should be used for dispersal decisions. However, if habitat capacity K_i is constant in time and environmental variations are driven by fluctuating reproductive rates $r = r_{i,t}$ (e.g., Poethke and Hovestadt 2002; Kun and Scheuring 2006), local resource competition $N_{i,t}/K_i$ may be the adequate information to be used. To avoid this confusion in the future, we suggest that it be clearly pointed out whether emigration decisions are (supposedly) based on estimates of population size ($N_{i,t}$), population density scaled to patch area ($N_{i,t}/A_i$)—which would be the appropriate measure of population density—or local (resource) competition ($N_{i,t}/K_{i,t}$). The definition of appropriate emigration response functions will necessarily also depend on the specific information animals may achieve before deciding on dispersal: patch quality and population size separately, more integrated variables such as intensity of resource competition, or just patch area or population size alone.

A principal merit in the work of Bocedi et al. is that the authors do not restrict their analysis to the extremes of purely spatial heterogeneity or purely uncorrelated temporal fluctuations, but their results are unfortunately obscured by the deficits named above. It is definitely misleading when

the authors predict an increase of emigration rates with increasing information. A comparable misinterpretation of results occurs in the recent modeling article of Rodrigues and Johnstone (2014). They claim that in temporally stable environments, habitat heterogeneity may select for negative density-dependent dispersal. They use population size synonymously with population density. However, in their model, no (local) habitat capacity is included; that is, there is no local density regulation. The evolutionary response they found is, in fact, a negative dispersal response to increased habitat quality and not to increased population density. Such a misleading and confused terminology is not a small issue, as theoretical articles often provide the basis for interpreting empirical studies or the design of experiments. In the case of informed dispersal, theoreticians must thus be careful in precisely communicating what kind of population model (regulation) they assume and what information they assume to be measured and in explaining and justifying the rules that link such information to dispersal decisions.

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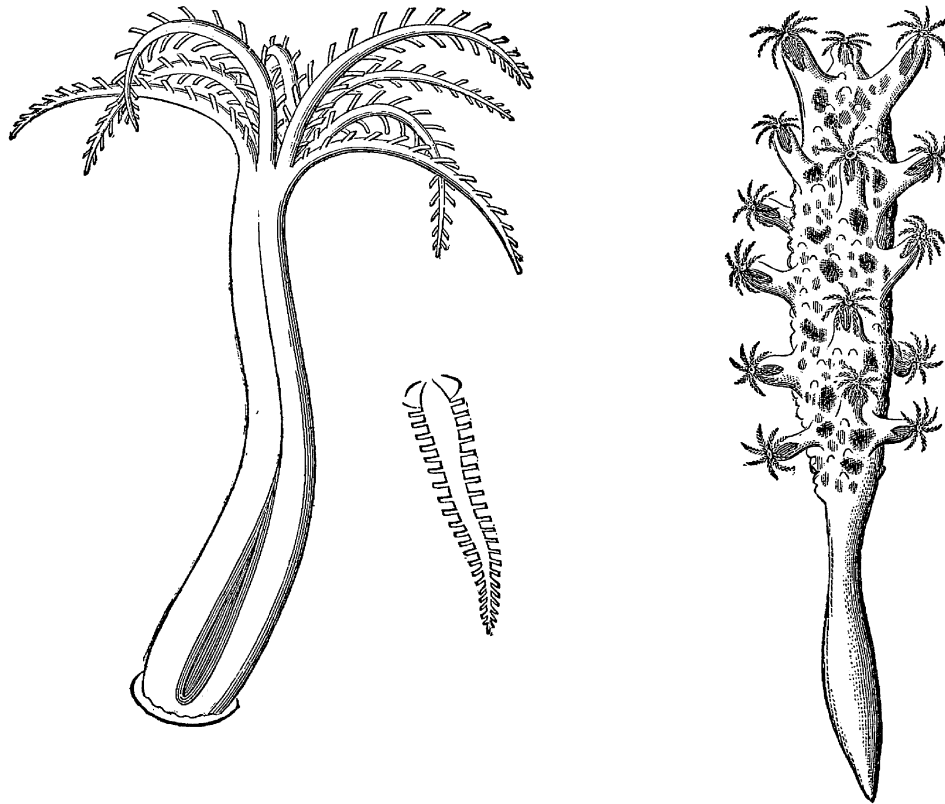
Left, Veretillum stimpsonii; center, single sea pen; *right*, whole colony of sea pens (*Kophobelemnon clavatum* V.). From the review of "Synopsis of the Polyps and Corals of the North Pacific Exploring Expedition, under Commodore C. Ringgold and Capt. John Rodgers, U.S.N., from 1853 to 1856, collected by Dr. Wm. Stimpson" (*The American Naturalist*, 1870, 4:488–491).