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Modeling density dependence in heterogeneous landscapes: Dispersal as a case study

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ABSTRACT

Population models often pose density-dependent rates as relations between current population size on a habitat patch, n, and some threshold size defined by limiting resources, r. In fourteen recent modeling studies incorporating density-dependent dispersal, formulations of the density-dependent rate (or probability) fall into two distinct groups, expressing the rate as a function of $n-r$ or n/r. These two depictions of the same process differ fundamentally: they can cause strikingly different dynamics in otherwise identical systems and they have different scaling properties in heterogeneous landscapes. Here I consider the implications of the two formulations under two broad ecological scenarios: scramble competition for an equally divided resource (e.g. food) and contest competition for an unequally divided resource (e.g. nest sites). In both cases, simple arguments show that the n/r form is preferable when density dependence is driven by individual access to resources. Other circumstances may require different formulations, but modelers must ensure that these have appropriate scaling and non-equilibrium behavior.

1. Introduction

Density dependence has an important influence on fecundity, survival, dispersal, and many other population processes. At the scale of a habitat patch, the effect of population density is typically felt relative to the supply of some limiting resource(s), such as food, space or nesting sites. As ecologists focus increasingly on the importance of landscape heterogeneity, it is essential that density-dependent rates are formulated such that they scale properly between habitat patches with different resource levels. I discuss this problem for the case study of dispersal rates, but the conclusions apply to other processes influenced by resource-driven density dependence.

While many factors can influence dispersal (Stenseth and Lidicker, 1992; Bullock et al., 2001; Clobert et al., 2001; Bowler and Benton, 2005), this paper addresses only the density-dependent component of the behavior. Per capita dispersal rates exhibit positive density dependence (i.e. higher density leads to increased dispersal) in mammals, birds, and insects (Denno and Peterson, 1995; Lambin et al., 2001; Sutherland et al., 2001; Rhainds et al., 2002; Matthysen, 2005), often due to insufficient resources in the local environment (Denno and Peterson, 1995; French and Travis, 2001; Lambin et al., 2001; Rhainds et al., 2002;

Bowler and Benton, 2005). Theoretical models have shown that evolutionarily stable strategies for dispersal should be density-dependent under almost all conditions, if local population densities are resource-limited (Travis et al., 1999; Poethke and Hovestadt, 2002).

Based on this evidence, many ecologists are incorporating density-dependent dispersal into mathematical models. At least fourteen recent studies present density-dependent dispersal as a relation between population size and resource level—but these models are not formulated consistently. To generalize notation across studies, let n_i be the population of the ith habitat patch, and r_i be its resource level (measured in the same units as n_i); r_i is often called the carrying capacity. Note that n_i is a dynamic variable, but r_i is assumed constant in these models. The fourteen papers then divide between formulating per capita rates or probabilities of density-dependent dispersal as functions of the difference n_i-r_i or of the ratio n_i/r_i (Table 1). These two formulations differ fundamentally. Certainly a function $f(n_i-r_i)$ can be cast as $f(n_i/r_i-1)$ by simply dividing the argument by r_i, but the slope or shape parameter (β or γ in Table 1) must be rescaled by a factor of r_i to compensate. In heterogeneous landscapes, r_i varies among patches so no single rescaling can be applied.

Here I address this inconsistency in model formulation, focusing on the different scaling properties of the two formulations in heterogeneous landscapes. I begin by demonstrating the potential impact of model formulation on dynamics and then consider the plausibility of the two formulations as depictions of resource-driven density dependence.

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Table 1
Per capita dispersal rates under the difference ($n_i - r_i$) or ratio (n_i/r_i) formulations, and studies that have used these forms.

	Per capita dispersal rate	References
Difference formulation		
Linear	$\alpha + \beta_{\text{diff}}(n_i - r_i)$	Doebeli (1995), Saether et al. (1999)[a,b]
Sigmoidal	$\dfrac{\delta}{1 + \exp[-\gamma_{\text{diff}}(n_i - r_i)]}$	Ives and Settle (1997)[a], Palmqvist et al. (2000), Ylikarjula et al. (2000), Kun and Scheuring (2006)[a]
Ratio formulation		
Linear	$\alpha + \beta_{\text{rat}}((n_i/r_i) - 1)$	Veit and Lewis (1996), Travis et al. (1999), French and Travis (2001)[a]
Sigmoidal	$\dfrac{\delta}{1 + \exp[-\gamma_{\text{rat}}((n_i/r_i) - 1)]}$	–
Other	Power function	Amarasekare (1998, 2004)[b], Best et al. (2007)
	Exponential	Johst and Brandl (1997)
	Hill function	Silva et al. (2001)[a]

Note: the population size and resource level of the ith patch are n_i and r_i, respectively; α and δ are constants scaling the dispersal rate in the linear and sigmoidal forms; and β and γ are slope and shape parameters for the linear and sigmoidal forms. All rate expressions are restricted to non-negative values. Functional forms may have been rearranged to bring n_i and r_i together, but are formally equivalent to the original expressions, and r_i was substituted for carrying capacity or other measures of threshold population size. Some density dependence expressions were originally posed as probabilities or in terms of population density, but as discussed in the text these cases are also addressed by the arguments in this paper.

[a] These studies did not consider heterogeneous landscapes or compare runs with different patch resource levels, so their findings are not influenced by their formulation of between-patch scaling. Kun and Scheuring (2006) consider r_i that vary by individual genotype but not by patch.
[b] These studies analyzed only continuous-time models, so the qualitative dynamics of their models are not influenced strongly by their choice of formulation. All other studies used discrete-time models, so qualitative effects on dynamics are possible.

1.1. Framing the discussion: definitions and assumptions

This paper uses a broad definition of dispersal as any movement between patches (Bowler and Benton, 2005), and addresses "when to leave" rather than "where to settle" (van Baalen and Hochberg, 2001). The resource level of a patch, r_i, sets the threshold population size against which density dependence is measured. Some authors define r_i phenomenologically via its effect on dispersal (e.g. as the inflection point for sigmoidal functions), while others use the steady state population size.

Note the assumptions implicit in models of this type. A single per capita rate is used for each patch, implying either that all inhabitants are identical and receive equal amounts of resource, or that heterogeneity in resource acquisition is implicitly averaged over the population. Most of these are single-species models, so impacts of predation, disease, or interspecific competition are not included; where other species are modeled, the interspecific interactions are decoupled from dispersal. Social behavior such as group cohesion or interference is not considered, nor are influences of relatedness and inclusive fitness. The landscape is assumed to be heterogeneous in space, but not in time.

All arguments presented below pertain to the behavior of individual animals and how it scales across heterogeneous landscapes. This reasoning is unaffected by shifting from continuous to discrete time, and conclusions regarding formulation apply equally to per capita rates and probabilities.

2. Dynamic consequences of different formulations

While apparently a minor distinction, use of the difference vs ratio formulation of density-dependent dispersal can significantly alter the overall dynamics produced by a population model. I demonstrate this using a simple multi-patch model that closely follows several studies cited in Table 1 (Ives and Settle, 1997; Palmqvist et al., 2000; Ylikarjula et al., 2000).

Consider a system of N patches in discrete time, where, in each time step, population growth occurs first, followed by dispersal. Population growth on each patch follows the classic Ricker model

(May and Oster, 1976):

$$n_i'(t) = n_i(t)\exp\left(\lambda\left[1 - \frac{n_i(t)}{r_i}\right]\right), \quad i = 1,\ldots,N \tag{1}$$

where $n_i(t)$ and $n_i'(t)$ are, respectively, the populations of the ith patch before and after demographic processes act, r_i is its resource level, and λ the intrinsic growth rate of the population. The per capita probability of dispersal from each patch, $f(n_i, r_i)$, is calculated from the sigmoidal forms in Table 1, using either the difference or ratio formulation. To compare the formulations, it is necessary to address the challenge noted in the Introduction section that they scale differently across heterogeneous patches. I address this by scaling the shape parameter γ_{rat} such that the "average" sensitivity of the two forms is comparable; two such scalings are employed, based on the mean resource levels calculated per patch and per individual (details in Fig. 1 caption). Dispersing individuals immigrate into all patches with equal probability—this is the "global dispersal" of Ives and Settle (1997). The population dynamics of the ith patch is given by

$$n_i(t+1) = n_i'(t) - f(n_i'(t), r_i)n_i'(t) + (1/N)\sum_{j=1}^{N} f(n_j'(t), r_j)\, n_j'(t) \tag{2}$$

where the three terms represent local reproduction, emigration, and immigration, respectively.

Sharply different dynamics can arise from the two model formulations (Fig. 1a, b), including some parameter ranges where the difference-formulated model predicts chaos while the ratio-formulated model (with per-patch scaling) predicts a stable equilibrium (e.g. around $\lambda = 1.3$) or a two-point cycle (e.g. $\lambda < 0.4$). When γ_{rat} is scaled by the per-individual mean resource level instead of the lower per-patch mean (Fig. 1c), the contrast between difference and ratio formulations is less dramatic but still distinct. The overall dispersal rate (averaged over 500 time steps) was similar across all formulations.

Results in Fig. 1 were selected to illustrate the disparities that can arise between the difference and ratio formulations, but similar qualitative distinctions are obtained for a wide range of parameter values, system structures, and functional forms for
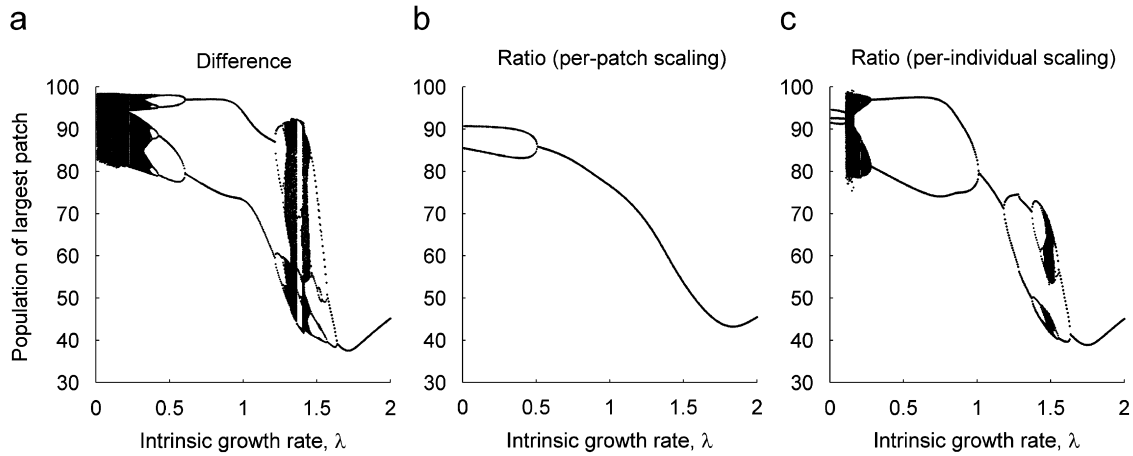
Fig. 1. Bifurcation diagrams for a 6-patch model using (a) difference and (b, c) ratio formulations of density-dependent dispersal. The shape parameter, γ_{rat}, of the sigmoidal density dependence function must be scaled such that the "average" sensitivity of the two formulations is comparable; results are shown for two scalings of the ratio formulation, where γ_{rat} is scaled based on the mean resource levels calculated (b) as a per-patch average (as $\gamma_{rat} = \gamma_{diff} \sum_{i=1}^{N} r_i/N$) or (c) as a per-individual average (as $\gamma_{rat} = \gamma_{diff} \sum_{i=1}^{N} (r_i)^2 / \sum_{i=1}^{N} r_i$). The population of the largest patch is shown as a function of the intrinsic growth rate, λ, of the Ricker logistic growth model governing patch demographics. Each patch began at $t=0$ with population equal to half its resource level, and the growth rate λ was identical on all patches. Bifurcation diagrams were constructed by iterating the system for 1000 time steps to allow transient dynamics to die out, then collecting and plotting population values for the next 500 time steps; this procedure was repeated for a range of values of λ. Parameter values were $\delta=0.8$, $\gamma_{diff}=0.5$, and $r_i=\{100,30,30,10,10,10\}$; using these r_i the values of γ_{rat} were $31.7\gamma_{diff}$ and $63.7\gamma_{diff}$ in panels (b) and (c), respectively. Populations of the smaller patches displayed similar dynamics.

density-dependent dispersal. The divergence between predictions of the difference and ratio forms is driven by landscape heterogeneity—discrepancies increase when resource levels of the patches are more diverse and diminish when the r_i are similar (Fig. 2). Discrepancies decrease for large values of the shape parameters, as the sigmoidal curves approach step

functions and dynamics become unstable for both formulations. Both formulations generate similar chaotic dynamics for $\lambda > 2.6924$, where the single-population Ricker model is known to exhibit chaos (May and Oster, 1976). Likewise, both forms yielded similar asymptotic approaches to equilibrium in a continuous-time analogue of the model presented above.
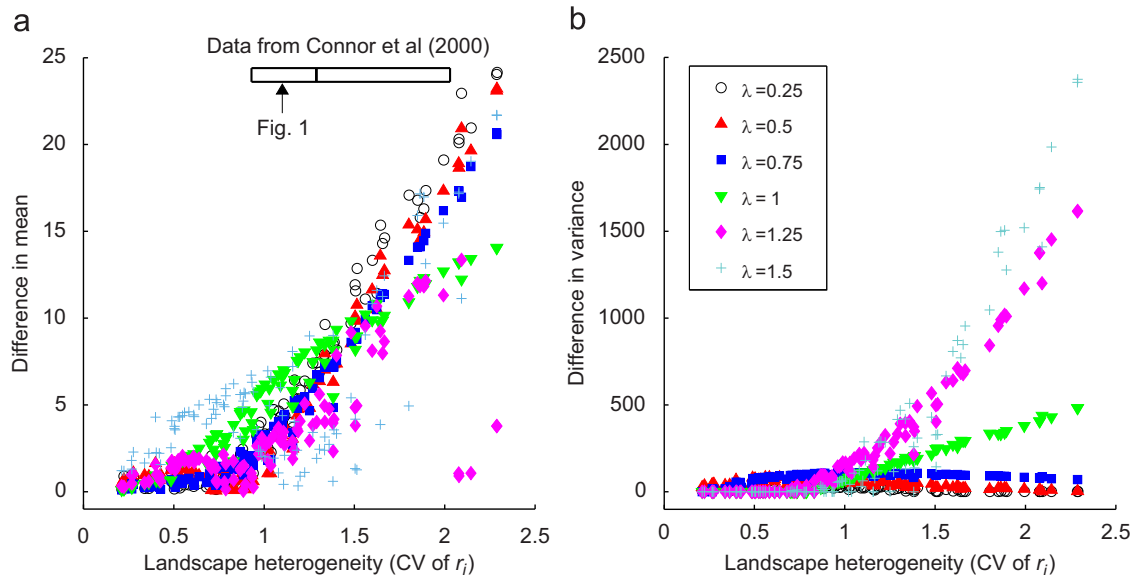
Fig. 2. Discrepancies between population dynamics predicted by the difference and ratio formulations of density-dependent dispersal. Plots show the difference in (a) mean and (b) variance of the population of the largest patch, for simulations conducted using the difference and ratio formulations of sigmoidal density dependent dispersal (i.e. the models used for Fig. 1a and b), as a function of landscape heterogeneity. For each value of λ, simulations were run for 100 randomly generated heterogeneous landscapes, each of which had six patches with random values of r_i such that $\sum_i r_i = 190$ as in the scenario studied in Fig. 1. For each simulation, the system dynamics were iterated for 1000 time steps to allow transient dynamics to die out; then the population of the largest patch was collected for the next 500 time steps. The mean and variance of these population series were calculated, and absolute difference between the two model formulations was plotted as a function of the coefficient of variation (CV) of patch size (i.e. standard deviation of r_i/mean of r_i). Inset in (a) is a box plot showing the interquartile range and median of CV values reported for patch sizes in 30 insect, mammal, and bird metapopulations (median CV=1.29, IQR [0.93, 2.03]; Connor et al., 2000), and the CV of the patch size values used to generate Fig. 1 is marked with an arrow.

3. Resource-driven density dependence

Given the potential influence on dynamics, care is warranted in choosing which model formulation better represents the desired biological mechanisms. I consider density dependence of per capita dispersal rates that is driven primarily by individual access to limiting resources. This accords with theoretical traditions of several fields related to dispersal—namely foraging behavior (Charnov, 1976; Koops and Abrahams, 2003), habitat selection (Fretwell and Lucas, 1970; Morris, 2003), and population ecology (Lomnicki, 1988; Slobodkin, 1992; Sutherland, 1996)—in which individual decisions are determined by individual experience.

3.1. Equal division of resources and scramble competition

The simplest assumption, seemingly implicit in models that assign a single rate to each patch, is that available resources are shared equally by all inhabitants of a patch. Such an assumption requires that all individuals have equal competitive ability, and that order of arrival in the patch is unimportant. It also requires that the limiting resource is freely divisible (e.g. food or space, but

not nest sites) and distributed evenly relative to the movement and perceptual abilities of foragers. The assumption of equal resource partitioning corresponds to scramble competition, because some resources are consumed by individuals who then disperse from the patch (cf. the original definition of scramble competition, with some resources "dissipated by individuals which obtain insufficient for survival"; Nicholson, 1954).

Interpreting the difference and ratio formulations for this scenario is straightforward. When resources are shared equally, the individual experience of resource acquisition is the per capita resource supply, r_i/n_i. The difference formulation is posed in terms of the absolute difference—totaled over the entire patch—between current population size and the threshold size set by resource availability, a quantity without a clear relationship to the per capita resource supply. In contrast, the ratio formulation captures the individual experience directly, as it poses density dependence in terms of the reciprocal of the per capita resource (i.e. n_i/r_i, corresponding to the number of foragers competing for each unit of resource).

Now consider the scaling behavior predicted by the two formulations on patches with different resource levels. The difference formulation (Fig. 3a) yields curves of equal steepness on all patches—an individual's sensitivity to increased population
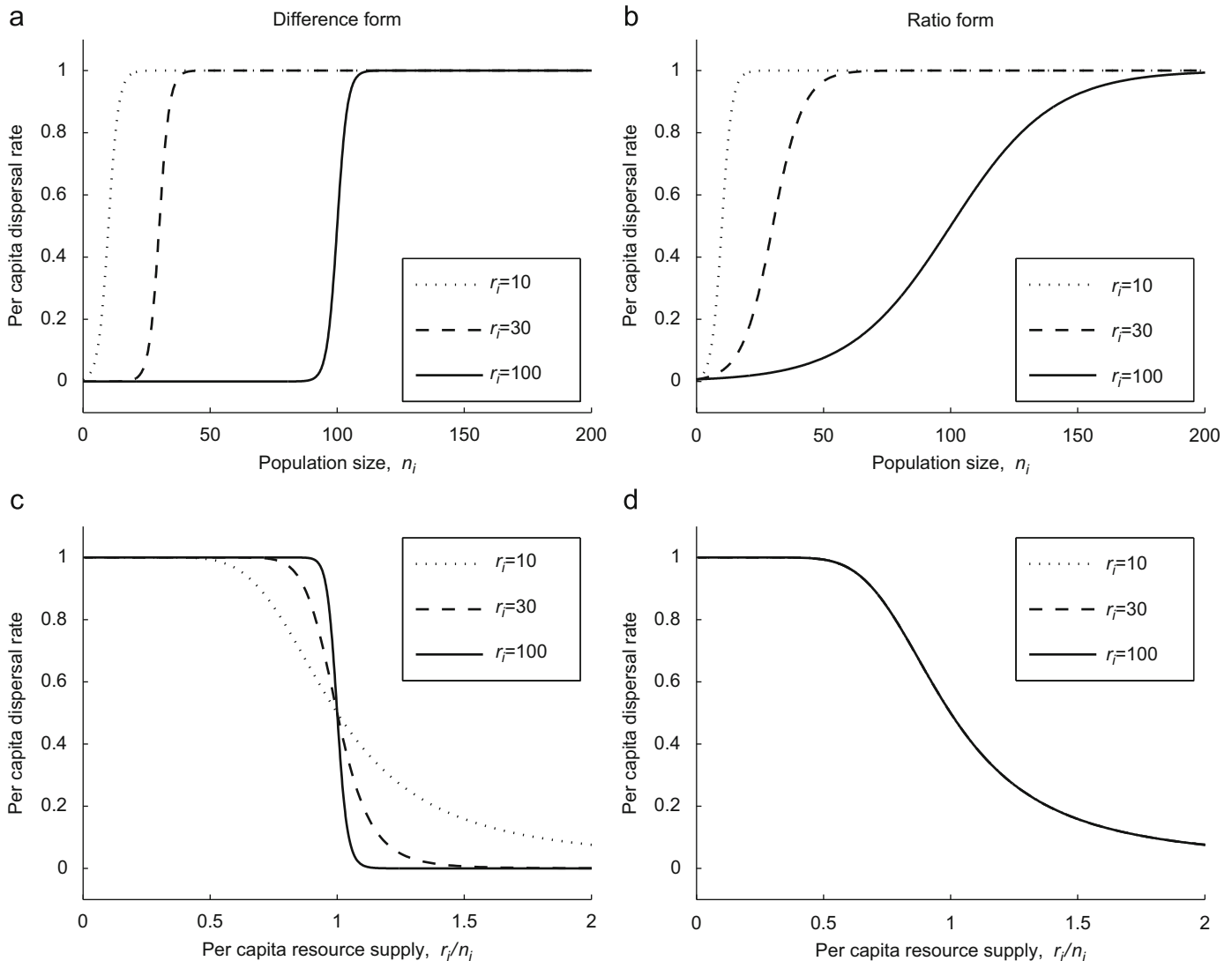
Fig. 3. Between-patch scaling of per capita rates vs (a, b) population size or (c, d) per capita resource supply under the (a, c) difference and (b, d) ratio formulations. Curves were calculated using the sigmoidal expressions in Table 1 with $\delta=1$, $\gamma_{\text{diff}}=0.5$, and $\gamma_{\text{rat}}=5$. (γ_{rat} has been scaled such that the ratio formulation $r_i=10$ curve is identical to that for the difference formulation. This has no effect on the arguments at hand, which pertain to the relative slopes of lines within each subplot.)

size (i.e. the change in per capita dispersal rate) is independent of the amount of resource being shared among the population. The ratio formulation (Fig. 3b) predicts that the sensitivity of dispersal rates to population size depends on resource level—individuals on resource-rich patches react less sharply to changes in n_i than individuals on resource-poor patches. Thus the ratio formulation captures the buffering effect of higher resource levels on per capita resource acquisition, while the difference formulation does not.

To further elucidate the different biological assumptions implied by the two formulations, consider their dependence on the per capita resource supply, r_i/n_i. The ratio formulation predicts that response to individual resource supply will be identical on all patches (Fig. 3d). This is logical for the simple (resource-driven, equal-competitor) models considered here, in which the per capita dispersal rate depends entirely on individual foraging success. In contrast, under the difference formulation, individuals on richer patches react more sharply to changes in r_i/n_i than those on poorer patches (Fig. 3c). This prediction is doubly implausible—not only are individuals predicted to respond differently to the same individual experience, but also foragers on the richest patches are inexplicably hyper-sensitive to increasing competition. Again we find that the ratio formulation yields more biologically reasonable predictions for how per capita rates—as motivated by individual experience—scale between patches in heterogeneous landscapes.

3.2. Unequal division of resources and contest competition

A more complex situation arises when the resource pool is divided unequally between individuals in a patch. This may occur for divisible resources such as food, when unequal competitors control different shares (Lomnicki, 1988; Koops and Abrahams, 2003), or for non-divisible resources such as nesting sites, where access is controlled pre-emptively by higher-ranking individuals (i.e. better competitors). These phenomena correspond to contest competition, because addition of lower-ranking individuals does not affect the resource supply of higher-ranking individuals (Lomnicki, 1988).

In the extreme case of unequally divided resources, all high-ranking individuals obtain sufficient quality or quantity of resources, but individuals beyond a certain population size receive no resources at all. This scenario corresponds to "saturation dispersal", in which all individuals up to a threshold number remain on a patch, while any further individuals—which fail to obtain resources—will disperse (Lidicker, 1975; Ruxton and Rohani, 1998; Poethke and Hovestadt, 2002; Bowler and Benton, 2005). Because $n_i - r_i$ individuals disperse in a given season, saturation dispersal at first resembles the difference formulation; however the experiences of all individuals must be averaged to calculate the per capita probability of dispersal. When $n_i \leq r_i$, no individuals disperse and the dispersal probability is zero. When $n_i > r_i$, $n_i - r_i$ out of n_i individuals will disperse, yielding an average per capita probability of $(n_i - r_i)/n_i = 1 - (n_i/r_i)^{-1}$. Therefore saturation dispersal is modeled by a ratio formulation. Less extreme instances of unequal resource partitioning, analyzed within a framework where rank determines resource access (Lomnicki, 1988), which in turn determines dispersal rate, also lead to ratio formulations (see Appendix).

4. Discussion

For two broad classes of intra-specific competition, I have argued that ratio formulations provide a better depiction of density dependence driven by individual access to resources than do difference formulations. Further issues remain, however. The choice of formulation is not dichotomous, as one could use a combination of the difference and ratio forms, or any other function of n_i and r_i. The functional form of the density-dependent rate expression (whatever function argument is used) is obviously important; linear and sigmoidal functions are used most commonly, but other options have been proposed (Table 1). The relative influence on dispersal of density-dependent and density-independent factors must be established. Ultimately, systematic analysis of the empirical relationship between population size, resource level, and dispersal is needed to conclusively resolve these issues of model formulation. In an encouraging first step, a recent study surveyed all available data and reported a near-universal pattern of nonlinearity in the density dependence of dispersal rates, though assessing the evidence for particular formulations is hampered by the lack of systematic reporting of resource levels (Kun and Scheuring, 2006).

A particular challenge is to understand density dependence in dispersal across different spatial scales. The mechanisms linking movement to resource availability are relatively clear at smaller scales, where foraging drives the process. Much less is understood about dispersal at larger scales. One recent review concluded that data are "simply insufficient" to properly assess landscape-level dispersal (South et al., 2001); another points out that causes of dispersal may vary with scale (Bowler and Benton, 2005). In density-dependent habitat selection, work on the role of dispersal costs and habitat use found opposite conclusions at small ("foraging") and large ("dispersal") scales (Morris, 1992). More empirical research on landscape-scale dispersal is clearly needed.

The two formulations discussed here can be distinguished further based on the capability of individual foragers to sense relevant quantities. Under the difference formulation, per capita dispersal rates are driven by the absolute difference, summed over the entire patch, between current population size and resource level. For the difference formulation to be realistic, individual foragers must be able to sense these conditions over the whole patch. The scale of information-gathering capabilities of the species in question, compared to the scale of landscape heterogeneity that drives patch size, will determine whether this is possible (vanBaalen and Hochberg, 2001). In contrast, the ratio formulation poses density dependence in terms of the number of foragers competing for each unit of resource (or equivalently in terms of the per capita resource supply), a quantity that can be sensed locally by individual animals. Arguments in favor of the ratio formulation thus align with the broader case made by Slobodkin (1992) that ecological models and theories should be posed in terms of intensive variables—those that do not depend on the extent of the system—because these variables reflect the local experience of individual animals.

An illustrative model demonstrated that the choice of difference vs ratio formulation of density-dependent dispersal has the potential to alter system dynamics dramatically (Figs. 1 and 2). Such qualitative distinctions in dynamics could distort the outcome of a modeling study, even a broader project in which density-dependent dispersal is a background component (Bowler and Benton, 2005). The present mixed use of the two formulations also introduces a confusing wildcard into on-going explorations of the effect of dispersal on metapopulation dynamics (Doebeli, 1995; Rohani et al., 1996; Amarasekare, 1998; Ruxton and Rohani, 1998; Ylikarjula et al., 2000; Silva et al., 2001; Doebeli and Killingback, 2003; Amarasekare, 2004; Ims and Andreassen, 2005), the evolution of dispersal (Hamilton and May, 1977; Holt and McPeek, 1996; Travis et al., 1999; Poethke and Hovestadt, 2002; Kun and Scheuring, 2006), and the impact of climate change on species survival and range shifts (Best et al., 2007). The tendency toward unstable dynamics under the difference formulation appears to arise from highly variable

dispersal fluxes generated by abrupt density dependence (i.e. steep curves near $n_i = r_i$) on large patches. In contrast, under the ratio formulation, density dependence sets in more gradually on larger patches so dispersal fluxes are more consistent.

Much of the present discussion generalizes to all population processes for which density dependence is driven by competition for limiting resources. Spatial heterogeneity continues to gain recognition as a determinant of ecological processes, and increasingly complex models are being used to synthesize field results and generate hypotheses. In heterogeneous landscapes, it is crucial that models be posed such that events and rates scale among habitat patches in a biologically reasonable way—we have seen that apparently benign differences in model formulation can have dramatic implications for system dynamics. When building density dependence into a model the full ramifications of functional form should be considered, including scaling among patches and behavior away from equilibrium (noting that the difference and ratio formulations diverge only when $n_i \neq r_i$). Ideally, authors should explain why a particular formulation has been chosen and what biological phenomena it is meant to represent, to enable clear and consistent progress in the ecology of heterogeneous landscapes.

Acknowledgements

Appendix. Dispersal rates when the resource pool is unequally divided

To discuss unequally divided resources, I introduce a more explicit interpretation of the resource level r_i. The resource controlled by each individual is scored from 0 to 1, where a score of 1 indicates fully satisfactory access to the resource (e.g. a high-quality nest site, or satiating supply of food), while a score of 0 corresponds to no resource at all. The patch resource level, r_i, is then defined as the sum of all these resource-access scores available on a patch. For example, if $r_i = 10$, there could be 10 nest sites of quality 1, or 4 sites of quality 1 and 12 sites of quality 0.5.

Now consider the general case of contest competition for an unequally divided resource pool. Following the formalism of Lomnicki (1988), each of the n individuals on a patch is assigned a rank x (where $x = 1$ is the highest rank, $x = 2$ is the second highest, etc.). The function $y(x|r)$ describes how the individual resource-access score varies with rank, on a patch with total resource pool r. Another function, $f(y)$, describes how the individual rate (or probability) of dispersal varies with individual resource-access score. For dispersal driven by competition for limiting resources, as discussed in this paper, $f(y)$ is a decreasing function. Note that $f(y)$ does not depend explicitly on x, n, or r; these variables affect f only through their influence on the resource-access score $y(x|r)$. In the argument that follows, the discrete quantity x is approximated as a continuous variable, because integration over x yields cleaner closed-form results than discrete summation. (Results obtained using discrete summation do not differ qualitatively from results shown below.) This limits the argument to a heuristic role, but allows it to be presented much more transparently.

The resource-vs-rank curves $y(x|r)$ obey three assumptions. First, the value of $y(x|r)$ is bounded on [0,1], where $y(x|r) = 1$ indicates access to a satiating quality or quantity of resource. Second, the curve is normalized such that the total resource available on the patch is r, i.e. $\int_0^\infty y(x|r)dx = r$. Finally the curve is non-increasing, because by definition higher-rank individuals have better access to resources. Six resource-vs-rank functions that obey these rules are shown in Fig. A1, with equations in Table A1. In all six cases, note that the equations include x and r only as a ratio, x/r. This was true for all functions $y(x|r)$ that I tested. Even deliberate attempts to choose functional forms for $y(x|r)$ that involve $x - r$ (curves d–f in Fig. A1) led to functions of $x|r$ after normalization.

The overall goal of this exercise is to calculate the mean per capita dispersal rate ($\bar{f}$) on each patch, under conditions of contest competition for unequally divided resources. Individual dispersal
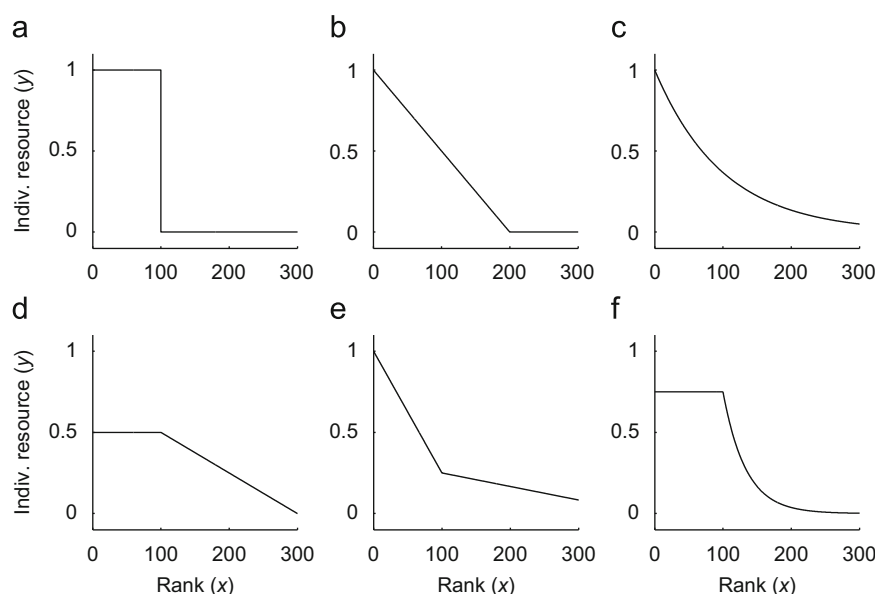

Fig. A1. Six possible resource-vs-rank curves, $y(x|r)$, for a patch with $r = 100$. Equations for the curves are shown in Table A1. Constants were $a = 0.5$, $b = 0.25$, and $c = 0.75$.

Table A1
Equations for the resource-vs-rank curves shown in Fig. A1.

Curve	$y(x/r)$ for $x \le r$	$y(x/r)$ for $x > r$
(a)	1	0
(b)[a]	$1 - x/2r$	0
(c)	$\exp(-x/r)$	$\exp(-x/r)$
(d)[b]	a	$a\left(1 - (a/(2(1-a)))((x/r)-1)\right)$
(e)[b]	$1 - bx/r$	$b\left(\left(1 - (b/1-b)\right)\left((x/r)-1\right)\right)$
(f)[b]	c	$c\exp(-(c/1-c)((x/r)-1))$

[a] The two columns correspond to $x \le 2r$ and $x > 2r$ for curve (b).
[b] The constants a, b, and c are bounded in the interval $(0,1)$.

rate may depend on resource access in a non-linear manner (i.e. f may be a non-linear function of y), so the mean per capita rate is

$$\overline{f} = (1/n)\int_0^n f\left(y(x|r)\right)dx$$

If, as described above, the variables x and r appear in $y(x|r)$ only as x/r, a new variable $u = x/r$ can be introduced. Recalling that r is constant on each patch, the mean per capita rate is then

$$\overline{f} = (r/n)\int_0^{n/r} f(y(u))du$$

For any integrable function $f(y(u))$, the indefinite integral will be some function of u. After evaluation at the limits $u = 0$ and $u = n/r$, $\overline{f}$ will be a function of n/r.

Therefore in the general case of contest competition for an unequally divided resource pool, subject to the stated assumptions, the mean per capita rate expression is always formulated in terms of the ratio n/r.

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