VOL. 195, NO. 5 THE AMERICAN NATURALIST MAY 2020

Frequency of Occurrence and Population-Dynamic Consequences of Different Forms of Density-Dependent Emigration

Rachel R. Harman,[1,*] Jerome Goddard II,[2] Ratnasingham Shivaji,[3] and James T. Cronin[1]

1. Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803; 2. Department of Mathematics and Computer Science, Auburn University at Montgomery, Montgomery, Alabama 36124; 3. Department of Mathematics and Statistics, University of North Carolina, Greensboro, North Carolina 27402

Submitted June 23, 2019; Accepted November 5, 2019; Electronically published March 18, 2020

Online enhancements: appendix, supplemental PDF.

ABSTRACT: Emigration is a fundamental process affecting species' local, regional, and large-scale dynamics. The paradigmatic view in ecology is that emigration is density independent (DIE) or positive density dependent (+DDE). However, alternative forms are biologically plausible, including negative (−DDE), U-shaped (uDDE), and hump-shaped (hDDE) forms. We reviewed the empirical literature to assess the frequency of different forms of density-dependent emigration and whether the form depended on methodology. We also developed a reaction-diffusion model to illustrate how different forms of DDE can affect patch-level population persistence. We found 145 studies, the majority representing DIE (30%) and +DDE (36%). However, we also regularly found −DDE (25%) and evidence for nonlinear DDE (9%), including one case of uDDE and two cases of hDDE. Nonlinear DDE detection is likely hindered by the use of few density levels and small density ranges. Based on our models, DIE and +DDE promoted stable and persistent populations. uDDE and −DDE generated an Allee effect that decreases minimum patch size. Last, −DDE and hDDE models yielded bistability that allows the establishment of populations at lower densities. We conclude that the emigration process can be a diverse function of density in nature and that alternative DDE forms can have important consequences for population dynamics.

Keywords: Allee effect, dispersal, movement model, negative density dependence, patch dynamics, population persistence.

Introduction

Emigration of organisms is a key process affecting colonization (Amarasekare 1998; Clobert et al. 2009), minimum patch size (Poethke and Hovestadt 2002), local densities, population stability (Hanski 1999), and species coexistence (Levins and Culver 1971; Cadotte et al. 2006). From a regional or metapopulation perspective, the magnitude of dispersal affects spatial synchrony and is fundamental to population persistence (Anholt 1995; Hanski 1999; Hanski and Gilpin 1997; Ims and Yaccoz 1997) and range expansion (Altwegg et al. 2013). As in the classic work of Levins (1969), early metapopulation models assumed density-independent emigration (DIE; e.g., Levins 1974; Pacala and Roughgarden 1982; Shmida and Ellner 1984; Hanski and Gilpin 1991). However, the more widely accepted view of emigration behavior is that species should exhibit a positive relationship between conspecific density and emigration (+DDE; Amarasekare 2004; Bowler and Benton 2005; Matthysen 2012), and many subsequent models incorporated this form of emigration (e.g., Pulliam 1988; Sæther et al. 1999; Hovestadt and Poethke 2006). Alternative forms of density-dependent emigration (DDE), including negative density-dependent emigration (−DDE) and nonlinear forms such as U-shaped density-dependent emigration (uDDE) and hump-shaped density-dependent emigration (hDDE), are theoretically plausible (see fig. 1) but have received almost no attention in the literature (but see Amarasekare 2004).

Although DIE and +DDE are widely reported in the literature, there has not been a systematic review that examines the breadth and frequency of DDE forms that occur in nature. Moreover, we know very little about the population-dynamic consequences of −DDE (but see Sæther et al. 1999; Amarasekare 2004; Matthysen 2005; Rodrigues and Johnstone 2014), uDDE, and hDDE forms. Our study has three objectives. First, we describe each form of DDE in figure 1, provide biologically plausible explanations for its occurrence, and, where possible, report what is known about its population-dynamic consequences. Second, we conduct an extensive review of the published literature that examined the relationship between conspecific density and emigration from a patch and assessed the range

---

* Corresponding author; email: rachel_harman@outlook.com.

ORCIDs: Harman, https://orcid.org/0000-0003-3449-7054; Goddard, https://orcid.org/0000-0003-0869-5153; Cronin, https://orcid.org/0000-0001-7111-6412.

Am. Nat. 2020. Vol. 195, pp. 851–867.
DOI: 10.1086/708156

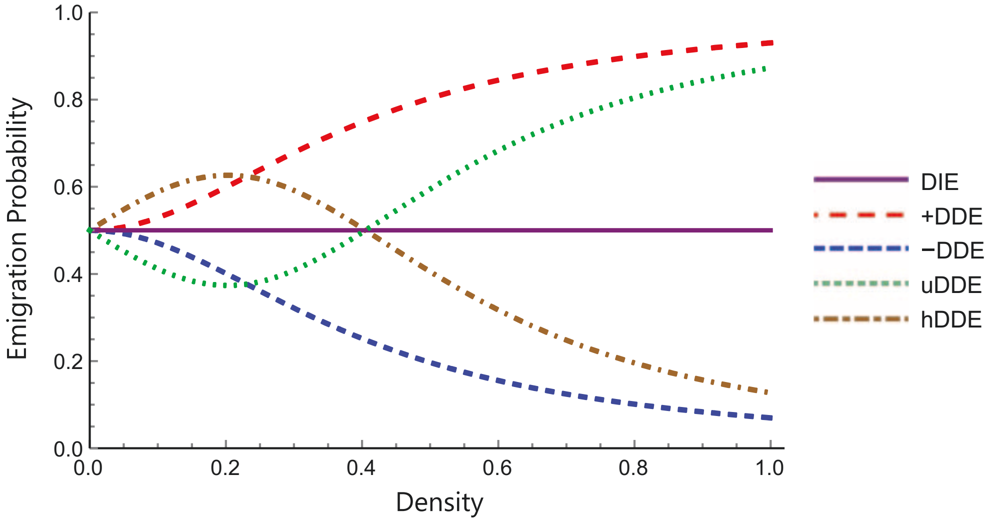

Figure 1: Hypothetical forms of the density-emigration relationship, including density-independent emigration (DIE), positive density-dependent emigration (+DDE), negative density-dependent emigration (−DDE), U-shaped density-dependent emigration (uDDE), and hump-shaped density dependent emigration (hDDE).

and frequency of different forms of DDE. Last, we develop a simple and flexible modeling framework based on reaction-diffusion equations to assess how the different forms of DDE affect population dynamics for a one-dimensional single-patch system with a matrix that has one of three hostility levels. Our intention with this model is to illustrate how each form of DDE can potentially influence the minimum patch size for population persistence, generate Allee effects, and affect population stability.

Objective 1: Forms of Density-Dependent Emigration

The evolution of +DDE (fig. 1) has been attributed to the population benefits of avoiding inbreeding and intraspecific competition (Hamilton and May 1977; Travis et al. 1999; Handley and Perrin 2007). As such, nongregarious species are expected to exhibit +DDE (Bowler and Benton 2005), as they receive little benefit from group living. Mathematical models predict that +DDE decreases the extinction probability in spatiotemporally variable environments (Amarasekare 2004). Theoretically, in nonstable environments, current patch quality does not determine future offspring value because resources are likely to change, leading to resource competition at high densities and promoting the evolution of +DDE strategies (Rodrigues and Johnstone 2014). Positive DDE may increase mean per capita fitness (Hovestadt et al. 2010), partially because the form promotes population growth in small populations, as dispersal probability is low (Amarasekare 2004).

In contrast, −DDE results in fewer individuals leaving at high densities (fig. 1), suggesting some benefit for species living in a group (Bowler and Benton 2005; Serrano et al. 2005; Kim et al. 2009; Matthysen 2012). Gregarious behavior in a population can underlie an Allee effect (Allee et al. 1949; Donahue 2006; Cantrell and Cosner 2007) and is often a consequence of the benefits of group living outweighing the costs of increased intraspecific competition, such as instances where conspecific attraction increases the chance of finding a mate (for a review, see Gascoigne et al. 2009), extra-pair mating opportunities (Serrano et al. 2005), defense against predators (Hammill et al. 2015), or foraging success (Kim et al. 2009). Under −DDE, the species is not expected to be resource limited at high density, but if it is, uDDE should arise (see below). With −DDE, population stability at the patch level has been shown to increase with an increase in growth rate (Sæther et al. 1999). Last, −DDE is likely to evolve in stable environments with constant habitat quality, as individuals residing in high-quality patches will constantly produce offspring with high fitness that are unlikely to leave at high densities (Rodrigues and Johnstone 2014).

Positive and negative DDE have distinct population-dynamic consequences at the metapopulation or regional scale. Positive DDE species have a greater chance of establishing a new population, as they are less likely to leave a previously unoccupied patch while their densities are low (Sæther et al. 1999). Therefore, +DDE species are expected to have a larger range than −DDE species, but range expansion may be faster in −DDE than +DDE species, as the former species emigrate more readily from unfavorable habitats that predominately contain low population densities (Altwegg et al. 2013). Range speed may also increase, as −DDE is more likely to evolve low dispersal costs and consequently higher dispersal rates (Rodrigues and Johnstone 2014). Conversely, the +DDE relationship will be the strongest when the cost of dispersal is greatest (Travis et al. 1999). Over the entire metapopulation, −DDE species should have a higher probability of local population extinctions, as individuals are more likely to leave the patch when densities are low; however, in the small range of occupied patches, extinction risk will be reduced (Sæther et al. 1999).

Very little attention has been given to nonlinear forms of density-dependent emigration, despite early recognition of its potential importance (e.g., Johst and Brandl 1997; Travis et al. 1999). For uDDE, the initial negative slope and high emigration rate at low density can be caused by the same factors that promote an Allee effect (Allee et al. 1949; Kim et al. 2009; Matthysen 2012; Altwegg et al. 2013). However, at high densities the negative effects of conspecific density, such as competition, encourage emigration. This combination of unfavorable effects of density has been noted in blue footed boobies (Kim et al. 2009) and strains of ciliated protozoa *Tetrahymena thermophila* that are highly aggregative (Jacob et al. 2016).

Last, hDDE has not been considered in any theoretical treatise. Biologically, this form could exist when the benefits of living in small and large groups are greater than intermediate-sized groups. For example, small groups may be less noticeable to predators, while larger groups may be more defensible; thus, intermediate-sized populations are less advantageous. With some genetic strains of ciliates, Jacob et al. (2016) found +DDE at low to intermediate density levels, but in larger populations emigration was reduced, potentially owing to bottlenecks in the movement through narrow corridors.

Objective 2: Presence of DDE Forms in the Literature

Methods

We compiled a database of emigration studies that were found in the Web of Science (http://www.webofknowledge.com). The search included all records in the database up to January 2, 2019. We used the search terms "density dependent dispersal," "density dependent emigration," "density independent emigration," "density independent dispersal," and "dispersal" plus "density." Review articles and relevant references from the collected articles were also searched. Articles were retained from the database if they (1) included data on emigration, (2) were empirically based (either experimental or observational), (3) used two or more conspecific density levels, and (4) had a study organism that engaged in active dispersal. We retained studies with only two density levels, but we acknowledge that those cases necessarily preclude the detection of nonlinear DDE (e.g., uDDE and hDDE). Although passive dispersal (e.g., transport by wind or water currents) can be density dependent (e.g., Kellner and Hubbell 2018; Sugiyama et al. 2018), we focused our study on species whose individuals make their own decision on when to leave on the basis of local density, patch size, boundary conditions, matrix composition, and so on.

Our Web of Science search yielded 115 articles on the relationship between conspecific density and emigration. Several of these articles included data for more than one species or multiple tests for the same species (e.g., for different age classes or stages, different sexes, or in response to different environmental contexts). For articles that subjected species to different treatments and reported more than one form of DDE, we treated each type of DDE for that species as an independent replicate in our analysis. We did this because we were most interested in the range of DDE forms, and averaging within a species could be misleading. Based on these criteria, we had 145 studies of DDE (see the appendix, available online).

Among the case studies, emigration was quantified in a number of ways: as the proportion leaving the patch (76% of studies), dispersal distance (18%), genetic relatedness (3%), and proportion of alates or macropters (3%). The proportion emigrating from a patch is a direct measurement of the emigration rate, and although it is the metric most often used, these other measurements are often regarded as good proxies for emigration. Dispersal distance is often used with species that emigrate from the natal habitat (e.g., from a nest; Molina-Morales et al. 2012). The genetics of a population measures DDE by calculating the relatedness of the individuals among patches (e.g., Van Hooft et al. 2008) or the distance separating full siblings (e.g., Derosier et al. 2007). Last, in some insects the proportion of long-winged individuals (macropters) in a population can be used as an index of dispersal capability (Denno et al. 2001). The production of macropters has been positively correlated with conspecific density in a number of insect species (e.g., Strong and Stiling 1983; Poniatowski and Fartmann 2011).

For each study, the relationship between emigration and density was assigned to one of five DDE forms: DIE, +DDE, −DDE, uDDE, or hDDE. Assignment was based on the authors' demonstration of a statistical relationship between density and emigration (e.g., regression, ANOVA, general linear mixed model). Unless the authors had already done so, if there were three or more density levels, we reanalyzed the data to test for nonlinearities in the density-emigration relationship. In all such cases ($n = 40$), we extracted the data from the original figures and analyzed the relationship between density and emigration using a nested set of predictor variables (constant only, constant +

density, constant + density + density^2). The Akaike information criterion corrected for small sample size (AICc) was used to choose the best model to explain variation in emigration and therefore determine the most likely form of DDE. The model with the smallest AICc value was deemed best, but all competing models with an AICc value within 2 of the best model were considered to have substantial support (Burnham et al. 2011). The analyses were performed using the statistical package mcmcplots in RStudio (RStudio Team 2016). Seven of the cases were reclassified as either uDDE or hDDE on the basis of this model selection procedure. The appendix and supplemental PDF identify which cases we found a different form of DDE than reported by the authors.

Quadratic regression is not a rigorous method for determining whether a relationship is truly U- or humped-shaped as opposed to being monotonically concave or convex (Simonsohn 2018). For the above seven reclassified cases and four of the six cases originally classified as hDDE and uDDE (we could not obtain the raw data for two cases), we used the Robin Hood algorithm proposed by Simonsohn (2018) that estimates two regression lines and tests whether there is a significant sign change between the slopes.

Similar to the review by Sibly et al. (2005) that explored the relationship between density and the per capita population growth rate, we also examined whether the form of DDE varied with taxonomic group. Species were grouped according to broad taxonomic classes (insect, mammal, bird, fish, reptile, other invertebrate, and microorganism). Because of low sample size, reptiles ($n = 4$ cases) were not included in subsequent taxonomic statistical analyses. We also assessed whether the frequency of each form of DDE differed between observational or experimental studies and whether the number of density levels or the range of densities influenced the detection of any particular form of DDE. For the density range, we took the ratio of the highest and lowest densities in the study. Finally, because of low sample sizes, all nonlinear forms of DDE, including uDDE and hDDE, were combined into the category “nonlinear” for methodological comparisons (number of densities, study method, and density ratio).

To evaluate whether the proportion of each DDE form varied significantly with taxonomic group or study methods (observational/experimental), we used separate Pearson’s χ^2 tests for independence with Monte Carlo simulations of 10,000 iterations. Differences among DDE forms in the number of density levels and density ratio were assessed with generalized linear models. To account for the right-skewed data and excess of low values, the error distribution was defined as negative binomial. χ^2 statistical analyses were performed with RStudio. The generalized linear models were analyzed using SAS version 9.4 (SAS Institute, Cary, NC). Proc GLIMMIX and all other analyses were performed with JMP version 14 (SAS Institute). Figures were created using JMP.

Results

Overall, the 145 case studies of DDE spanned a wide range of taxa, including insects (43%), mammals (15%), birds (16%), fish (8%), invertebrates (10%), microorganisms (6%), and reptiles (2%). As predicted, the majority of cases exhibited +DDE (36%) or DIE (30%) forms. Interestingly, −DDE was reported in 25% of the cases. Finally, 6% and 3% of the cases were classified as uDDE and hDDE, respectively. These nonlinear forms of DDE have been reported only since 2009; however, four cases of uDDE and hDDE predating 2009 were reclassified by us (see the appendix). Following more rigorous testing using the Robin Hood method of Simonsohn (2018), we could confirm only one case of uDDE (Maag et al. 2018) and two cases of hDDE (Jacob et al. 2016; Chatelain and Mathieu 2017; table S2; tables A1, S1–S3 are available online).

We found no evidence that the frequencies of different forms of DDE varied among taxonomic group ($\chi^2_{20} = 19.81$, $P = .47$; fig. 2). However, the frequencies of each form of DDE did depend on whether the study was observational or experimental (38% and 62% of all studies, respectively). Cases reporting DIE and +DDE were significantly more likely to be experimental than observational: 72% of the cases of DIE and 69% of the cases of +DDE occurred in experimental studies (for DIE, $\chi^2_1 = 19.36$, $P < .0001$; for +DDE, $\chi^2_1 = 14.44$, $P = .0001$). Conversely, 58% of −DDE cases were observational studies ($\chi^2_1 = 4.0$, $P = .046$). Finally, the 13 nonlinear cases had methods equally shared between observational (43%) and experimental (57%) methods ($\chi^2_1 = 0.98$, $P = .32$).

Among the 145 case studies in our review, the number of densities or density levels were often quite low. Twenty-two percent of the cases had only two densities, and an additional 21% had three. Not surprisingly, observational studies averaged more than twice as many densities as the experimental studies (14.4 ± 3.1 [median, 7.0] vs. 5.9 ± 0.7 [median, 3.5]; $F_{1,129} = 29.2$, $P < .001$; fig. 3). Additionally, the range of densities, measured as the ratio of the highest to the lowest density, was 1.2 times greater for observational studies (21.4 ± 6.0 [median, 6.3]) than experimental studies (17.6 ± 4.0 [median, 6.0]; $F_{1,121} = 29.9$, $P < .001$; fig. 3). The number of densities was significantly different among DDE forms ($F_{3,127} = 5.66$, $P = .001$; fig. 3), with cases of DIE (5.2 ± 0.6 [median, 5.0]) utilizing a third of the densities of cases of nonlinear DDE (14.3 ± 6.8 [median, 4.0]) and half the densities of cases of +DDE (8.3 ± 1.4 [median, 4.0]) and −DDE (11.0 ± 3.1 [median, 5.0]). The number of densities was also significantly higher for nonlinear DDE cases than +DDE cases

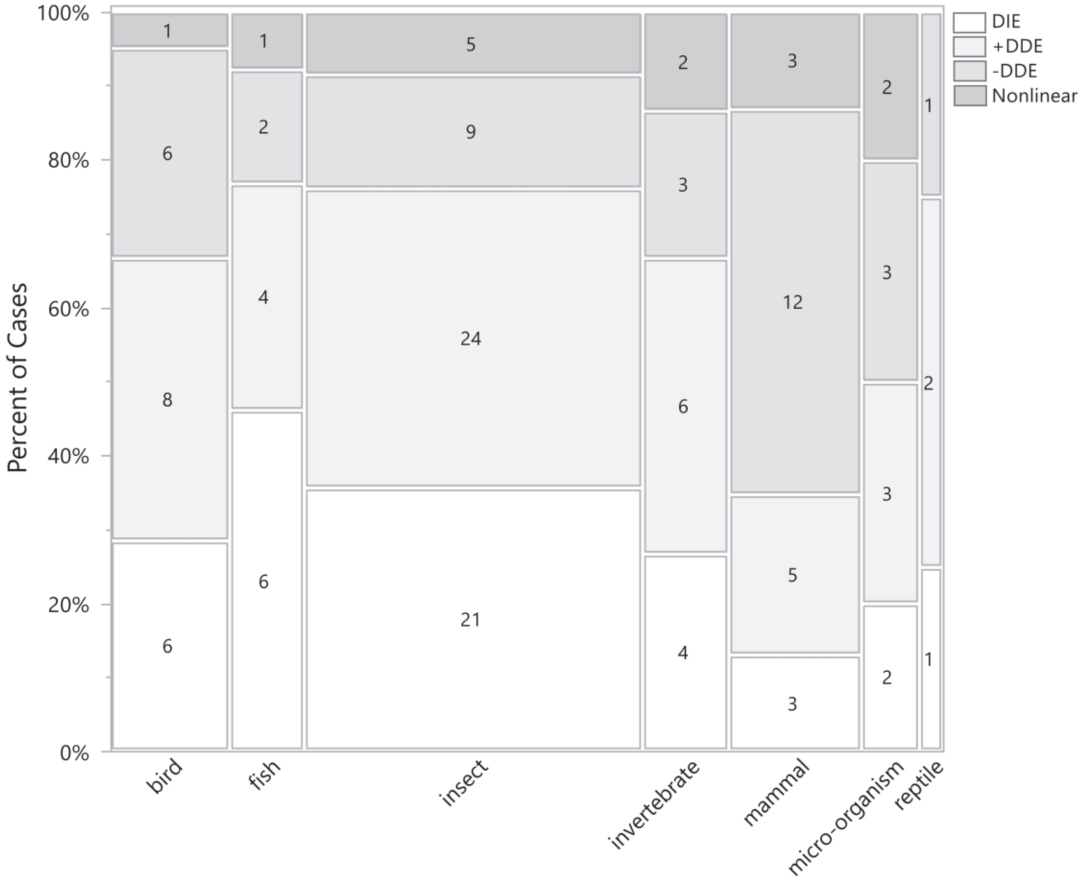

Figure 2: Mosaic representing the percentage of each density-emigration form within taxonomic group. Numbers represent the number of cases within each category. The width of each column represents the proportion of each taxon among all cases. The density-emigration forms include density-independent (DIE), positive (+DDE), negative (−DDE), and nonlinear forms (U-shaped, hump-shaped, and all forms with a significant quadratic term in the model combined).

($P = .05$). DIE cases also utilized a narrower range of densities than the other DDE forms ($F_{3,119} = 5.77, P = .001$; fig. 3). Studies with DIE had a high density–to–low density ratio of 9.1 ± 2.6 (median, 4.0). Studies with +DDE, −DDE, and the nonlinear forms had a ratio of 25.7 ± 7.8 (median, 7.5), 17.3 ± 4.1 (median, 8.0), and 24.2 ± 8.0 (median, 16.0), respectively (fig. 3).

Objective 3: Population Dynamics of DDE

Methods

Although a wide range of DDE forms are evident in nature, little is known about the long-term population consequences for populations that exhibit each form. To illustrate the key differences in population persistence and minimum patch size between the DDE forms, we mathematically analyzed a theoretical population model based on the reaction-diffusion framework. Our flexible one-patch model allows patch size, boundary condition, and matrix hostility to vary with a defined form of DDE (fig. 4). This approach is not an exhaustive analysis of the local population-dynamic consequences of different forms of DDE; however, we demonstrate, with a broadly applicable model, that the form of DDE can have important consequences for within-patch population dynamics, such as population persistence in patches that meet a minimum patch size (Schultz and Crone 2005).

Edge permeability can be dependent on the matrix surrounding the patch (Reeve et al. 2008), as matrix degradation increases mortality of dispersers (Maciel and Lutscher 2013); therefore, we utilize three matrix hostility levels to assess population persistence. First, we consider a one-dimensional patch $\Omega = (0, \ell)$ surrounded by a hostile matrix, where $\ell > 0$ represents the patch size. The model is based on a derivation given in Cronin et al. (2019) and the references therein. Here, $u(t, x)$ represents the density of a theoretical population (u) inhabiting patch Ω, with the

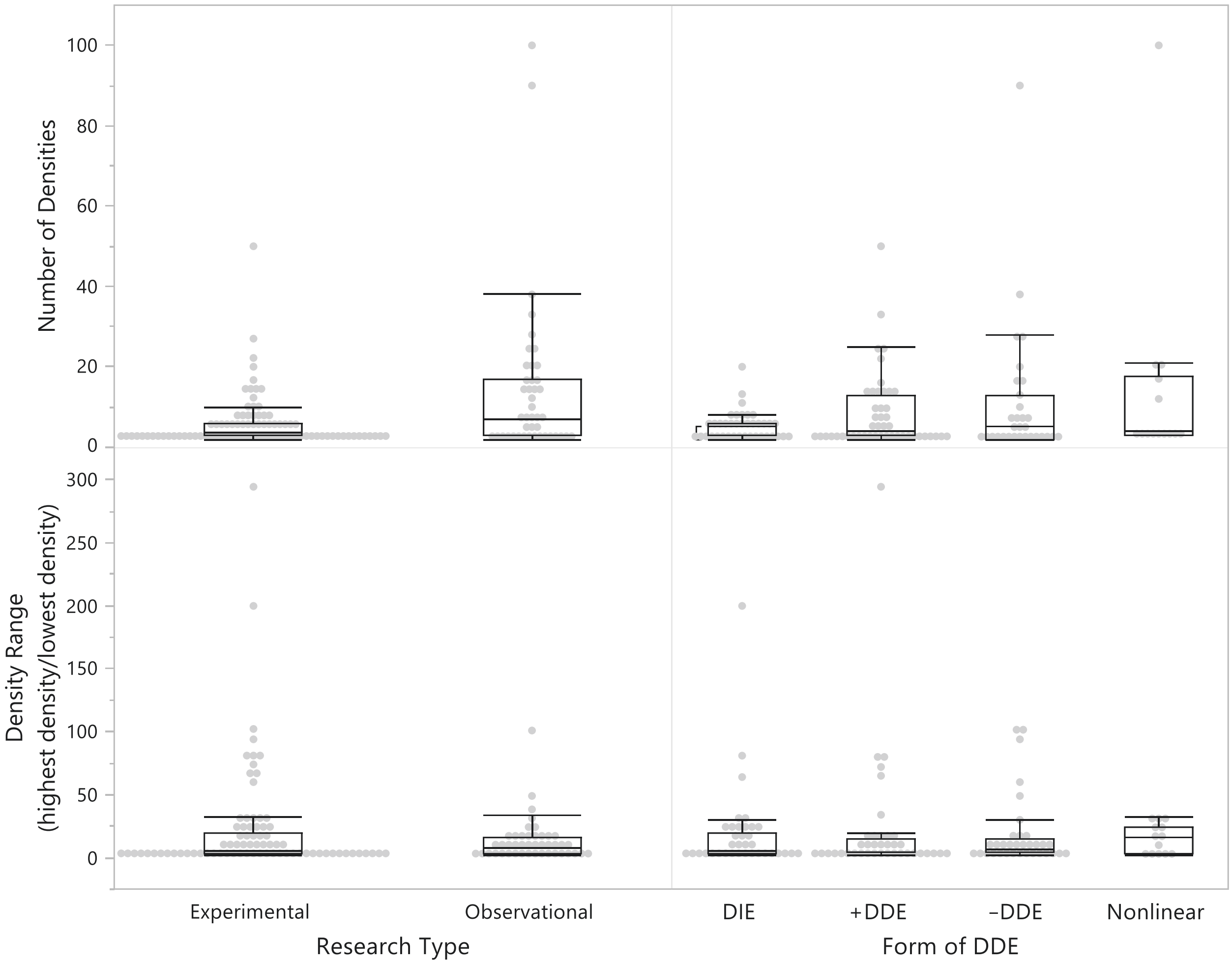

Figure 3: Box-and-whisker plots for the number of density levels and density range for experimental and observational methods as well as for the different forms of density-dependent emigration (DDE; density independent [DIE], positive [+DDE], negative [−DDE], and all nonlinear forms combined). Each boxplot shows the median (horizontal bar) and the 25% and 75% quantiles (ends of the box). Whiskers are ±1.5 (range between the 25% and 75% quantiles). Gray points are the raw data.

variable t representing time and x representing spatial location. The model is then

$$\begin{aligned} u_t &= Du_{xx} + ru\left(1 - \frac{u}{K}\right), \quad t > 0,\ x \in \Omega, \\ D\alpha_i(u)\frac{\partial u}{\partial \eta} &+ \frac{\sqrt{S_0 D_0}}{\kappa}[1 - \alpha_i(u)]u = 0, \quad t > 0,\ x \in \partial\Omega, \end{aligned} \tag{1}$$

where the parameter D is the diffusion rate inside the patch, D_0 is the diffusion rate in the matrix surrounding the patch, S_0 is the death rate in the matrix, $\alpha_i\colon [0, \infty) \to [0, 1]$ encodes the DDE relationship as a function of organism density that outputs the probability that an organism remains in the patch on reaching the boundary $(\partial\Omega)$ with $i = 1, 2, 3, 4$, or 5 depending on the density-emigration relationship, and κ is a parameter encapsulating assumptions (see Cronin et al. 2019) regarding the patch/matrix interface, such as movement behavior. Also, $\partial u/\partial \eta$ represents the outward normal derivative of u, and the reaction term is standard logistic growth with intrinsic growth rate r and carrying capacity K of the population inside the patch, Ω. The parameters D, D_0, S_0, r, K, and κ are always positive. The dynamics of equation (1) with constant α_i and $\kappa = 1$ are well known (see, e.g., Cantrell and Cosner 2003).

Following a standard nondimensionalization, equation (1) becomes

$$\begin{aligned} u_t &= \frac{D}{r\ell^2}u_{xx} + u(1 - u), \quad t > 0,\ x \in \Omega_0, \\ \alpha_i(u)\frac{\partial u}{\partial \eta} &+ \ell\gamma[1 - \alpha_i(u)]u = 0, \quad t > 0,\ x \in \partial\Omega_0, \end{aligned} \tag{2}$$

where the patch size ℓ is now present as a parameter inside the model, $\Omega_0 = (0, 1)$, $u(t, x)$ now measures a percentage

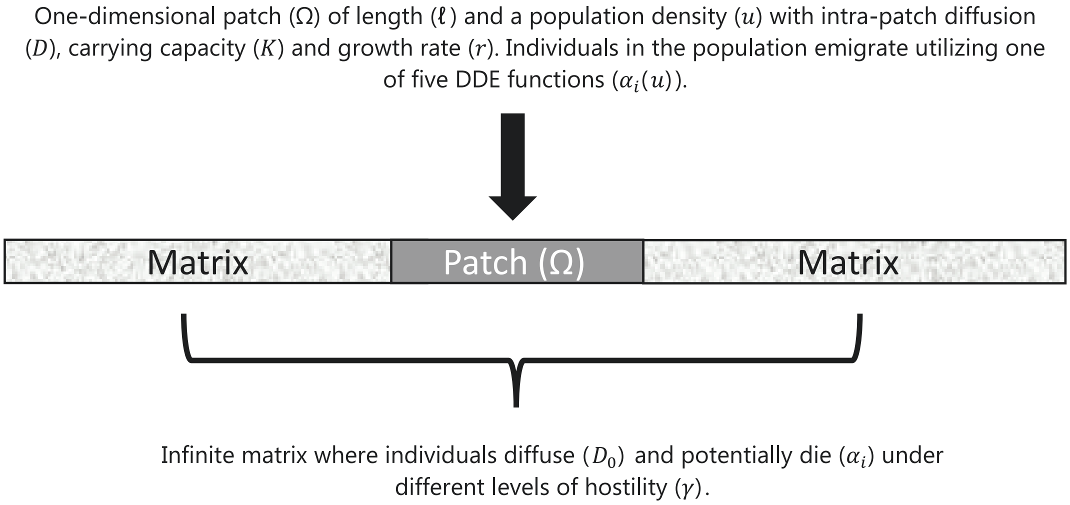

Figure 4: Graphic representation of the primary variables incorporated into the one-patch model used to create the bifurcation-stability curves for each form of density-dependent emigration (DDE).

of the carrying capacity K, t has been scaled by the intrinsic growth rate r, and $\gamma = (S_0D_0)^{1/2}/(D\kappa)$ describes the hostility of the matrix where $\gamma \approx 0$ implies a low level of hostility and $\gamma \gg 1$ implies a situation where an organism faces almost immediate mortality upon entering the matrix. Last, through the nondimensionalization process, κ has an impact only on the interpretation of the matrix hostility, γ, and does not qualitatively change the bifurcation-stability curves resulting from the model. Using these important parameters found in equation (2), we can illustrate the potential dynamical differences between the DDE forms in a clear, generalizable reaction-diffusion model.

To assess the effects of different DDE forms on the persistence of a population with dynamics that are governed by equation (1), five $\alpha_i(u)$ functions were selected, with $\alpha_1(u)$, $\alpha_2(u)$, $\alpha_3(u)$, $\alpha_4(u)$, and $\alpha_5(u)$ representing DIE, +DDE, −DDE, uDDE, and hDDE, respectively (for details, see the supplemental PDF, available online). Each $\alpha_i(0)$ value is designed so that any corresponding differences in the results are due only to the density-emigration relationship. We then employed an adaptation of the time-map analysis method given in Foneska et al. (2019) to study the structure of positive steady-state solutions of equation (2), that is, the conditions under which population persistence is possible. An algorithm was written in Mathematica version 11.2 (Wolfram Research) to generate bifurcation curves based on this method, which depicts the structure of positive steady states (i.e., population persistence) of equation (2) as the main parameters patch size, ℓ, and matrix hostility, γ, are varied. The time-map analysis method and resulting bifurcation curves provide a complete picture of the number and types of positive steady states for equation (2).

To augment these bifurcation curves, we performed a linearized stability analysis of the trivial steady state of population extinction, $u(x) \equiv 0$, and determined the stability properties of this state, including the location of the state's change from stable to unstable, based on the parameters in the model. Furthermore, we employed the time-map analysis method and Mathematica version 11.2 (Wolfram Research) to computationally determine the actual profile of each steady state. A linearized stability analysis was then used on these steady-state profiles to numerically estimate the stability properties of each steady state. The final product of this analysis is a bifurcation-stability curve of the patch size ℓ versus the maximum value of the steady-state profiles with an indication of whether each steady state is stable or unstable for each fixed γ (matrix hostility). Note that all stable steady states are asymptotically stable.

Results

We fixed values for the intrinsic growth rate, r, and patch diffusion rate, D, and produced bifurcation-stability curves for three scenarios: (1) low matrix hostility $\gamma \approx 0$, (2) intermediate matrix hostility, and (3) high matrix hostility $\gamma \gg 1$. The scenarios of low matrix hostility (see the supplemental PDF) and intermediate hostility (fig. 5) yielded qualitatively similar model predictions.

In all cases of matrix hostility, there is a minimum patch size, denoted as ℓ^*, for each of the forms of DDE. For any patch with a size larger than ℓ^*, the model predicts that any nonnegative initial density profile will tend to a positive steady state as time $t \to \infty$ and lead to unconditional persistence. Depending on the form of DDE and patch size, the steady state may be precariously close to zero, and

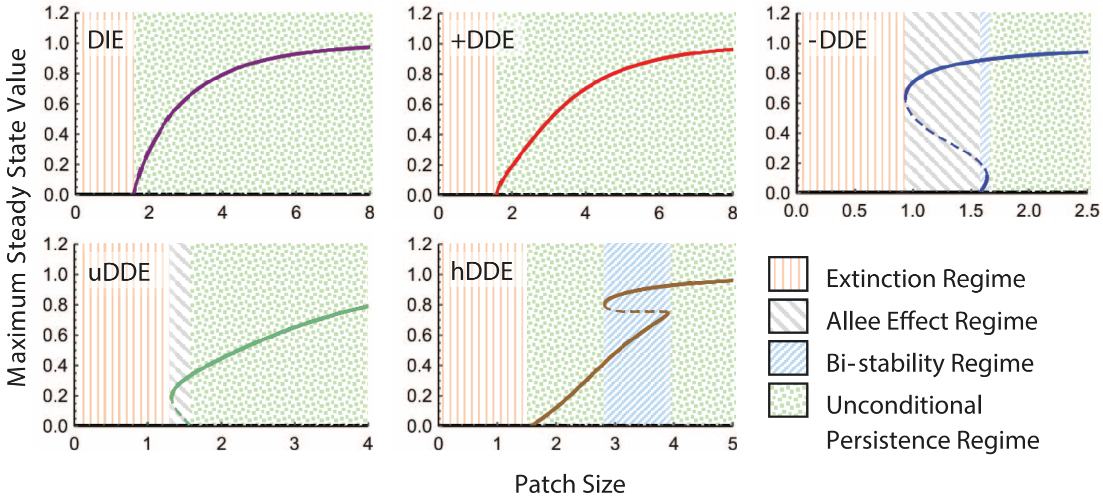

Figure 5: Bifurcation-stability curve of population persistence within an intermediate hostility matrix. Solid curves indicate stable steady states, and dashed curves indicate unstable steady states. The density-emigration forms include density independent (DIE), positive (+DDE), negative (−DDE), U-shaped (uDDE), and hump-shaped (hDDE). Note that the scaling of the *X*-axis differs among density-dependent emigration forms to more clearly show Allee and bistability regimes.

the local population may be prone to extinction given a large enough stochastic event that negatively affects the population. For patches whose size is below the minimum patch size ℓ^*, population persistence depends on the density-emigration relationship and proximity of the actual patch size to ℓ^*. In all cases of matrix hostility, sufficiently small patches are predicted to become extinct ($u \equiv 0$) and patch sizes greater than π are predicted to have unconditional persistence, as there is enough core size to ensure that the effects of the hostile matrix are mitigated. Specifically, for a hostile matrix (fig. 6), there is no change in the minimum patch size between the DDE forms.

For both a low (supplemental PDF) and an intermediate (fig. 5) hostility matrix, for DIE, +DDE, and hDDE, ℓ^* is exactly the minimum patch size for the population to persist. Below this threshold patch size, successful colonization would not be possible and the population would become extinct. For patches whose size is greater than ℓ^*, the model predicts unconditional persistence for any positive initial density profile. However, populations with patch

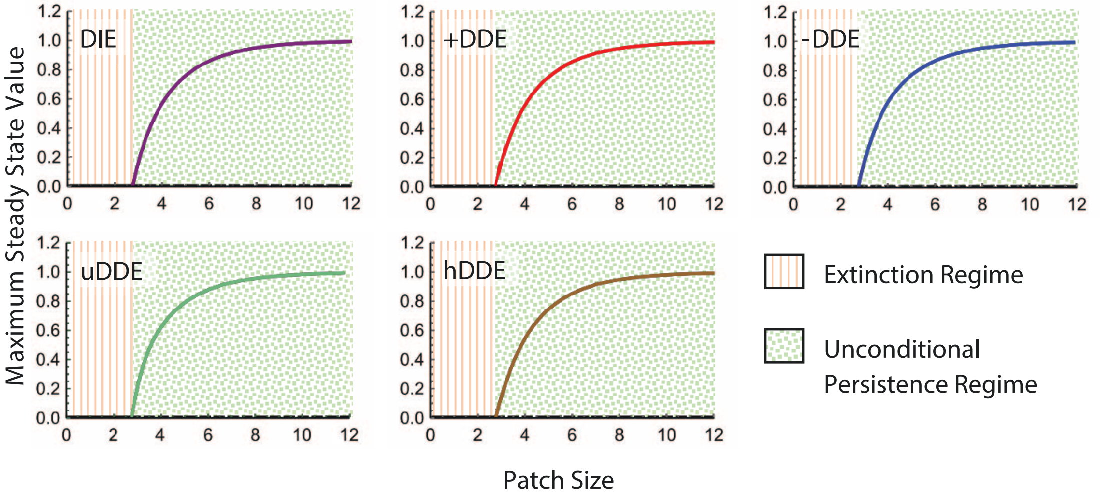

Figure 6: Bifurcation-stability curve of population persistence within a high-hostility matrix. Solid curves indicate stable steady states. The density-emigration forms include density independent (DIE), positive (+DDE), negative (−DDE), U-shaped (uDDE), and hump-shaped (hDDE).

sizes below ℓ^* but sufficiently close to ℓ^* have conditional persistence. The model predicts an Allee effect for patches with this size range (Allee effect regime) for the −DDE and uDDE forms. An Allee effect arises in a reaction-diffusion model whenever the trivial state (zero population size) and a positive steady state are both stable with at least one unstable state separating the basin of attraction for these stable states. For patches whose size is below the Allee effect regime, the model predicts population extinction. In patches with larger size, a monostability regime exists with predictions of unconditional persistence.

When matrix hostilities are low (supplemental PDF) and intermediate (fig. 5), populations with −DDE forms are predicted to exhibit bistability in patches with sizes larger than ℓ^* but sufficiently close to it. Likewise, a similar bistability region exists in the case of hDDE for patches with sizes slightly larger than ℓ^*. The bistability region predicts two positive steady states that are stable, with an unstable state partitioning the basin of attraction for these stable states.

For a high hostility matrix, the theoretical organism has a high probability of dying on leaving the patch. Within this severe environment, the model predicts a minimum patch size ℓ^* ($\ell^* \approx 2.7$; fig. 6) that is the same for each of the forms of DDE and is larger than each of the intermediate and low hostility matrix landscapes. However, for patches with sizes greater than ℓ^*, the model predicts population persistence. In such a high hostility matrix, the model predicts very little dynamical differences between density-emigration forms.

Discussion

Ecological theory has been rather limited in its view of how density influences emigration. Although our literature review confirmed that +DDE and DIE are the most common forms of density-dependent emigration (36% and 30% of the cases, respectively), −DDE accounted for 25% of the cases, and nonlinear forms (uDDE and hDDE) accounted for another 9% of the cases. Importantly, our models suggest that these nonparadigmatic forms of DDE (−DDE, uDDE, and hDDE) can cause interesting and complex within-patch dynamics that are not observed when considering only traditional forms of DDE. Specifically, our models reveal the possibility of Allee effects that can cause a decrease in minimum patch size, allow populations to persist in very small patches, and cause populations to suddenly crash if the patch is further reduced in area. Forms of DDE that have negative density-dependent emigration at high densities (−DDE and hDDE) can also have two steady states within smaller patches.

We suggest that negative and nonlinear forms of DDE are more common than our literature review has revealed. Studies tend to use very few density levels, particularly experimental studies. In fact, 22% of the 145 studies used only two density levels, thus precluding the detection of nonlinear DDE. Another 21% of the studies used only three density levels, the absolute minimum number needed to detect nonlinearities in the density-emigration relationship. Necessarily because of the replicated nature of experimental studies, the number of density levels is often small. In the case of our literature review, experimental studies used one-half as many density levels as observational studies, with a median of only 3.5 density levels. Furthermore, our analysis of the literature revealed that studies reporting evidence for DIE had a density range, measured as the ratio of the highest to the lowest density level, that was one-half the range used to detect the other forms of DDE. The ability to detect density dependence in any of its forms (e.g., density-dependent per capita growth) has long been known to be limited by sample size, number of densities, or range of densities (e.g., Hassell 1986; Fowler et al. 2006). Of course, these methodological limitations have been recognized by those who study species emigration. For example, the Glanville fritillary butterfly (*Melitaea cinxia*) was reported as having both −DDE and +DDE (Kuussaari et al. 1996; Kuussaari et al. 1998). By combining results from these two studies and effectively expanding the density range, Enfjall and Leimar (2005) concluded that uDDE was a better fit for this species. Clearly, future observational studies and experiments should include a broader range and number of densities to better characterize this relationship.

Models have predicted that −DDE creates unstable populations in which population density is poorly regulated and thus unlikely in nature (Wolff 1997; Amarasekare 2004). Despite this theoretical disadvantage to populations, −DDE was found in one-fourth of the studies. At least over a portion of the density range, −DDE is expected for species actively engaged in group living (Bowler and Benton 2005; Kim et al. 2009; Matthysen 2012). Intuitively, we would expect that as the density of a gregarious species gets too high, increased rates of emigration should follow (i.e., uDDE). Examples of a gregarious species exhibiting −DDE include the sociable weaver (*Philetairus socius*; Altwegg et al. 2014) and prairie voles (*Microtus ochrogaster*; Smith and Batzli 2006). In another interesting example, Jacob et al. (2016) established genetic lines of the ciliated protozoa *Tetrahymena thermophile* that displayed either low, medium, or high degrees of aggregation. Those lines exhibited hDDE, −DDE, and uDDE, respectively. We attempted to explore whether gregarious species were predisposed to exhibiting −DDE or uDDE. However, for many species it was impossible to categorize them in a binary way as either solitary or gregarious, and there was insufficient information from the literature to divide them by degree of gregariousness.

In addition to life-history effects on DDE (see above), the form of DDE can also be phenotypically plastic and a function of predispersal conditions. For example, longer exposure time to a higher number of conspecifics led to stronger −DDE in fruit flies (*Drosophila melanogaster*; Mishra et al. 2018). These high-density environments could increase the stress of the individuals (Mishra et al. 2018) or provide ample opportunity for mates (for a review, see Kokko and Rankin 2006), decreasing emigration at high densities. Also, trophic interactions can promote gregarious behaviors, such as with the ciliate *Paramecium aurelia*, which changed from +DDE to −DDE in the absence and presence of predator cues, respectively (Hammill et al. 2015). This change in emigration strategy is theoretically dependent on the predator-induced increase in costs of dispersal that outweigh the benefits of emigrating (Hammill et al. 2015). However, this change in the form of DDE is likely system dependent; the opposite result (+DDE) occurred for the backswimmer *Notonecta undulata* when predator cues were present (Baines et al. 2014).

Density-dependent emigration is an important factor that affects population persistence (Anholt 1995; Hanski 1999). In our model, both DIE and +DDE achieve a similar asymptotic stable state as patch size increases. This stability is inherent in standard population growth models and allows for local population persistence as emigration increases when densities reach carrying capacity (Dethier 1964). Populations near their carrying capacity would tend to favor the occurrence of DIE and +DDE and could explain why those two forms were found in two-thirds of all of the cases we examined. Constant population persistence, however, is not universally found in nature (e.g., Turchin and Taylor 1992). Models have incorporated nonlinear density-dependent emigration, which can increase or decrease population persistence times (Amarasekare 1998), change minimum patch size (Colombo and Anteneodo 2018), and affect the stability of predator-prey systems (Hauzy et al. 2010). To our knowledge, no other models have examined completely convex or concave uDDE and hDDE nonlinear response curves, which we show have more complex ecological consequences than nonlinearity alone.

Alternative forms of DDE change the persistence of populations within small patches with low to intermediate matrix hostility. The Allee effect regime found in populations with −DDE and uDDE allows populations to persist in smaller patches than the other forms of DDE. However, population persistence and reproductive success change at minimum patch sizes (Butcher et al. 2010), particularly for area-sensitive species (Qing et al. 2016). As only a large population is able to persist in the Allee effect patches in our model, colonization by few individuals is unlikely to create a new population in these tiny patches. Divided populations from a newly fragmented large patch are the most likely inhabitants, which is why anthropogenic fragmentation is one of the leading causes of demographic Allee effects found in populations (Courchamp et al. 2008). The Allee effect is often connected with gregarious species that receive a benefit from cohorts (Kramer et al. 2018). Interspecifically, the Allee effect has been shown to induce multistability in predator-prey systems (Dhiman and Poria 2018). Although Allee effects are considered widespread, have been found in many taxa (Dennis et al. 2016), and could become more commonplace as our global climate warms (Kramer et al. 2018; Berec 2019), little empirical work has examined how Allee effects are directly caused by dispersal and habitat alteration (Kramer et al. 2009). Dispersal between populations with strong Allee effects allows for population persistence (Wang 2016); however, populations in patches that are close to the minimum patch size are likely to crash because of stochastic events or minute decreases in the size of the patch. This has dire consequences for conservation biology, as populations that appear to have high fitness may suddenly become extinct once they hit the extinction threshold in our model.

Similarly, the negative slope of −DDE and uDDE changes the reaction norm and produces bistability regimes that allow the organism to colonize and persist at a much lower density level than the other DDE forms. The different attractors create alternative stable states and can create great fluctuations in population abundance that can result in population extinction (Sutherland 1990; Petraitis and Dudgeon 1999). Most empirical work with alternate stable states has been performed with passive dispersing plants (e.g., Bertness et al. 2002) or examining entire ecosystem shifts (e.g., Van De Koppel et al. 2001; van de Leemput et al. 2016). There is some empirical evidence of population bistability in either gregarious or −DDE species, such as the southern pine beetle (Martinson et al. 2013), Indo-Pacific sea urchin (Han 2016), and *Daphnia* (Nelson et al. 2001); however, emigration has not been directly connected to alternative stable states. This may be due to the lack of appropriately conducted studies, the majority of which focus on environmental changes as a treatment and do not report dispersal (for a review, see Schroder et al. 2005) or studies that focus on pest eradication instead of population persistence (e.g., Martinson et al. 2013).

The scale at which the study is performed can determine the density-emigration relationship measured. For example, in peregrine falcons (*Falco peregrinus*) natal dispersal distance was density independent at local scales but negatively related to density on a regional scale (Morton et al. 2018). A limited spatial scale may exclude long-distance dispersers, resulting in altered density-emigration relationships (Morton et al. 2018). Additionally, density may be heterogeneous across a landscape, and these differences in population density may affect dispersal decisions (Bitume et al. 2013) or promote aggregation only in highly suitable habitats (e.g., damselflies; Allen and Thompson 2010) that could lead to a false positive for −DDE. Finally, density-dependent dispersal decisions (e.g., avoidance of inbreeding or competition) may differ as costs and benefits of dispersing vary with spatial scale (Bowler and Benton 2005). However, few studies have examined density dependence at various spatial scales (but see Bowler and Benton 2005; Kim et al. 2009; Morton et al. 2018).

For some species, the decision to emigrate may depend on exploratory forays into the matrix. If "foray loops" are common, as some studies with butterflies, birds, and mammals suggest (e.g., Rivera et al. 1998; Roper et al. 2003; Conradt and Roper 2006), experiments that immediately remove individuals that exit the patch may overestimate emigration and predict spurious forms of DDE. Based on our literature survey, 14% of the experimental studies used this approach (appendix; 6 cases of DIE, and 7 cases of +DDE). If the goal is to characterize the density-emigration relationship, we recommend allowing foray loops to occur or documenting that they are uncommon.

Many patch- or regional-level DDE models do not consider matrix hostility, but the choice to emigrate, and thus population persistence, can be dependent on the quality of the matrix (Roland et al. 2000; Cronin and Haynes 2004; Cronin 2007). In high-hostility matrices, each of the DDE bifurcation-stability curves has unconditional persistence, which is partially due to the high mortality in the matrix greatly decreasing the chance that emigrating individuals will reenter the patch. Additionally, the minimum patch size is greater in patches surrounded by a more hostile matrix due to a greater edge effect. The decrease in patch area creates a decrease in the percentage of the patch that is unaffected by the edge due to the ratio of edge to patch area (Laurance 1991), ecologically creating a smaller patch despite the area (Fagan et al. 1999). As a more hostile matrix creates a stronger edge, the core of the patch correspondingly must be larger for a population to persist. However, once a core density is reached, population persistence is stable (Cronin 2009) and there is little need for rescue from other populations.

The alternative forms of DDE create metapopulations that have more diverse interactions. In −DDE and hDDE, the innate Allee effect can decrease the rate of range expansion, creating a stable range (Amarasekare 1998; Wang 2016). As habitat is increasingly becoming more fragmented, the ability of populations to persist in smaller patches (as seen with −DDE and hDDE) may decrease the likelihood of metapopulation extinction. These small patches can then be used as stepping-stones, which are crucial for long-distance range expansion (Saura et al. 2014), especially for −DDE species that are more likely to emigrate at low densities. A highly hostile matrix, however, will minimize the chances of rescue or colonization of patches, which will increase chances of extinction (Vandermeer and Carvajal 2001) and decrease range expansion speed. Last, change in the strength of the Allee effect can change the rate of range expansion, creating models that over- or underpredict the actual speed (Walter et al. 2017). Understanding both environmental and intrinsic density-dependent factors will better predict the movement of invasive species and metapopulation persistence in a fragmented landscape.

Conclusions

Although our literature review supports the view that density-independent and positive density-dependent emigration should be most common in nature, we found negative density-dependent emigration in one-fourth of the cases and nonlinear density dependence in another 9% of the cases. Because studies often include few density levels or focus on a relatively narrow range of densities, nonlinear forms of DDE may have gone undetected. Methods that incorporate a greater number and range of density treatments in addition to using more rigorous nonlinear statistics could improve the chances of detecting these forms. Primarily, research should focus on regression-based experimental designs that incorporate both very low densities and those at and above carrying capacity. Life history (e.g., gregariousness) as well as different dispersal conditions (e.g., temporal variability and environmental cues; Baines et al. 2014; Hammill et al. 2015) should be addressed or manipulated to assess plasticity in behaviors that might promote different forms of DDE. Last, statistics should incorporate not only quadratic analyses but also more flexible models capable of detecting a wider range of nonlinear forms, such as uDDE or hDDE (e.g., Simonsohn 2018). As our simple analytical model suggests, understanding these DDE forms can be critical for estimating population persistence, particularly in small patches. For example, rarely considered forms of DDE (−DDE, uDDE, and hDDE) yield Allee effects and bistability regimes that are not inherent in the more well-known forms of DDE (i.e., DIE and +DDE). These new population dynamics can lead to important biological consequences, such as population extinction and changes in source-sink dynamics.

Acknowledgments

We thank Jeremy Fox and Alice Winn as well as the anonymous reviews for their insightful comments that helped us greatly improve this article. This research was supported by National Science Foundation grants DMS-1516833, DMS-1516560, and DMS-1516519 to J.T.C., G.D., and R.S., respectively, and by a grant from the Louisiana Environmental Education Commission to R.R.H.

Literature Cited

Allee, W. C., O. Park, A. E. Emerson, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. Saunders, Philadelphia.

Allen, K. A., and D. J. Thompson. 2010. Movement characteristics of the scarce blue-tailed damselfly, *Ischnura pumilio*. Insect Conservation and Diversity 3:5–14.

Altwegg, R., Y. C. Collingham, B. Erni, and B. Huntley. 2013. Density-dependent dispersal and the speed of range expansions. Diversity and Distributions 19:60–68.

Altwegg, R., C. Doutrelant, M. D. Anderson, C. N. Spottiswoode, and R. Covas. 2014. Climate, social factors and research disturbance influence population dynamics in a declining sociable weaver metapopulation. Oecologia 174:413–425.

Amarasekare, P. 1998. Interactions between local dynamics and dispersal: insights from single species models. Theoretical Population Biology 53:44–59.

———. 2004. The role of density-dependent dispersal in source-sink dynamics. Journal of Theoretical Biology 226:159–168.

Anholt, B. R. 1995. Density-dependence resolves the stream drift paradox. Ecology 76:2235–2239.

Baines, C. B., S. J. McCauley, and L. Rowe. 2014. The interactive effects of competition and predation risk on dispersal in an insect. Biology Letters 10:20140287.

Berec, L. 2019. Allee effects under climate change. Oikos 128:972–983.

Bertness, M. D., G. C. Trussell, P. J. Ewanchuk, and B. R. Silliman. 2002. Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? Ecology 83:3434–3448.

Bitume, E. V., D. Bonte, O. Ronce, F. Bach, E. Flaven, I. Olivieri, and C. M. Nieberding. 2013. Density and genetic relatedness increase dispersal distance in a subsocial organism. Ecology Letters 16:430–437.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews 80:205–225.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23–35.

Butcher, J. A., M. L. Morrison, D. Ransom, R. D. Slack, and R. N. Wilkins. 2010. Evidence of a minimum patch size threshold of reproductive success in an endangered songbird. Journal of Wildlife Management 74:133–139.

Cadotte, M. W., D. V. Mai, S. Jantz, M. D. Collins, M. Keele, and J. A. Drake. 2006. On testing the competition-colonization trade-off in a multispecies assemblage. American Naturalist 168:704–709.

Cantrell, R. S., and C. Cosner. 2003. Spatial ecology via reaction-diffusion equations. Wiley Series in Mathematical and Computational Biology. Wiley, Chichester.

———. 2007. Density dependent behavior at habitat boundaries and the Allee effect. Bulletin of Mathematical Biology 69:2339–2360.

Chatelain, M., and J. Mathieu. 2017. How good are epigeic earthworms at dispersing? an investigation to compare epigeic to endogeic and anecic groups. Soil Biology and Biochemistry 111:115–123.

Clobert, J., J. F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197–209.

Colombo, E. H., and C. Anteneodo. 2018. Nonlinear population dynamics in a bounded habitat. Journal of Theoretical Biology 446:11–18.

Conradt, L., and T. J. Roper. 2006. Nonrandom movement behavior at habitat boundaries in two butterfly species: implications for dispersal. Ecology 87:125–132.

Courchamp, F., L. Berec, and J. Gascoigne. 2008. Allee effects in ecology and conservation. Oxford University Press, Oxford.

Cronin, J. T. 2007. From population sources to sieves: the matrix alters host-parasitoid source-sink structure. Ecology 88:2966–2976.

———. 2009. Habitat edges, within-patch dispersion of hosts, and parasitoid oviposition behavior. Ecology 90:196–207.

Cronin, J. T., J. Goddard II, and R. Shivaji. 2019. Effects of patch matrix and individual movement response on population persistence at the patch-level. Bulletin of Mathematical Biology 81:3933–3975.

Cronin, J. T., and K. J. Haynes. 2004. An invasive plant promotes unstable host-parasitoid patch dynamics. Ecology 85:2772–2782.

Dennis, B., L. Assas, S. Elaydi, E. Kwessi, and G. Livadiotis. 2016. Allee effects and resilience in stochastic populations. Theoretical Ecology 9:323–335.

Denno, R. F., D. J. Hawthorne, B. L. Thorne, and C. Gratton. 2001. Reduced flight capability in British Virgin Island populations of a wing-dimorphic insect: the role of habitat isolation, persistence, and structure. Ecological Entomology 26:25–36.

Derosier, A. L., M. L. Jones, and K. T. Scribner. 2007. Dispersal of sea lamprey larvae during early life: relevance for recruitment dynamics. Environmental Biology of Fishes 78:271–284.

Dethier, V. G., and R. H. MacArthur. 1964. A field's capacity to support a butterfly population. Nature 201:728–729.

Dhiman, A., and S. Poria. 2018. Allee effect induced diversity in evolutionary dynamics. Chaos Solitons and Fractals 108:32–38.

Donahue, M. J. 2006. Allee effects and conspecific cueing jointly lead to conspecific attraction. Oecologia 149:33–43.

Enfjall, K., and O. Leimar. 2005. Density-dependent dispersal in the Glanville fritillary, *Melitaea cinxia*. Oikos 108:465–472.

Fagan, W. E., R. S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. American Naturalist 153:165–182.

Foneska, N., J. Goddard II, Q. Morris, R. Shivaji, and B. Son. 2019. On the effects of the exterior matrix hostility and a U-shaped density dependent dispersal on a diffusive logistic growth model. Discrete and Continuous Dynamical Systems Series B, http://doi.org/10.3934/dcdss.2020245.

Fowler, N. L., R. D. Overath, and C. M. Pease. 2006. Detection of density dependence requires density manipulations and calculation of lambda. Ecology 87:655–664.

Gascoigne, J., L. Berec, S. Gregory, and F. Courchamp. 2009. Dangerously few liaisons: a review of mate-finding Allee effects. Population Ecology 51:355–372.

Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. Nature 269:578–581.

Hammill, E., R. G. Fitzjohn, and D. S. Srivastava. 2015. Conspecific density modulates the effect of predation on dispersal rates. Oecologia 178:1149–1158.

Han, X. Y. 2016. Persistent alternate abundance states in the coral reef sea urchin *Diadema savignyi*: evidence of alternate attractors. Marine Ecology 37:1179–1189.

Handley, L. J. L., and N. Perrin. 2007. Advances in our understanding of mammalian sex-biased dispersal. Molecular Ecology 16:1559–1578.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, New York.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics—brief history and conceptual domain. Biological Journal of the Linnean Society 42:3–16.

———. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, London.

Hassell, M. P. 1986. Detecting density dependence. Trends in Ecology and Evolution 1:90–93.

Hauzy, C., M. Gauduchon, F. D. Hulot, and M. Loreau. 2010. Density-dependent dispersal and relative dispersal affect the stability of predator-prey metacommunities. Journal of Theoretical Biology 266:458–469.

Hovestadt, T., A. Kubisch, and H. J. Poethke. 2010. Information processing in models for density-dependent emigration: a comparison. Ecological Modelling 221:405–410.

Hovestadt, T., and H. J. Poethke. 2006. The control of emigration and its consequences for the survival of populations. Ecological Modelling 190:443–453.

Ims, R. A., and N. G. Yaccoz. 1997. Studying transfer processes in metapopulations: emigration, migration, and colonization. Pages 247–265 *in* I. Hanski and M. E. Gilpin, eds. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego.

Jacob, S., P. Wehi, J. Clobert, D. Legrand, N. Schtickzelle, M. Huet, and A. Chaine. 2016. Cooperation-mediated plasticity in dispersal and colonization. Evolution 70:2336–2345.

Johst, K., and R. Brandl. 1997. Evolution of dispersal: the importance of the temporal order of reproduction and dispersal. Proceedings of the Royal Society B 264:23–30.

Kellner, J. R., and S. P. Hubbell. 2018. Density-dependent adult recruitment in a low-density tropical tree. Proceedings of the National Academy of Sciences of the USA 115:11268–11273.

Kim, S. Y., R. Torres, and H. Drummond. 2009. Simultaneous positive and negative density-dependent dispersal in a colonial bird species. Ecology 90:230–239.

Kokko, H., and D. J. Rankin. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. Philosophical Transactions of the Royal Society B 361:319–334.

Kramer, A. M., L. Berec, and J. M. Drake. 2018. Allee effects in ecology and evolution. Journal of Animal Ecology 87:7–10.

Kramer, A. M., B. Dennis, A. M. Liebhold, and J. M. Drake. 2009. The evidence for Allee effects. Population Ecology 51:341–354.

Kuussaari, M., M. Nieminen, and I. Hanski. 1996. An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. Journal of Animal Ecology 65:791–801.

Kuussaari, M., I. Saccheri, M. Camara, and I. Hanski. 1998. Allee effect and population dynamics in the Glanville fritillary butterfly. Oikos 82:384–392.

Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain-forest mammals. Conservation Biology 5:79–89.

Levin, S. A. 1974. Dispersion and population interactions. American Naturalist 108:207–228.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species (mathematical model/habitable patches). Proceedings of the National Academy of Sciences of the USA 68:1246–1248.

Maag, N., G. Cozzi, T. Clutton-Brock, and A. Ozgul. 2018. Density-dependent dispersal strategies in a cooperative breeder. Ecology 99:1932–1941.

Maciel, G. A., and F. Lutscher. 2013. How individual movement response to habitat edges affects population persistence and spatial spread. American Naturalist 182:42–52.

Martinson, S. J., T. Ylioja, B. T. Sullivan, R. F. Billings, and M. P. Ayres. 2013. Alternate attractors in the population dynamics of a tree-killing bark beetle. Population Ecology 55:95–106.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28:403–416.

———. 2012. Multicausality of dispersal: a review. Pages 3–18 *in* J. Clobert, M. Baguette, T. G. Benton, and J. M. Bullock, eds. Dispersal ecology and evolution. Oxford University Press. Oxford.

Mishra, A., S. Tung, V. R. S. Sruti, M. A. Sadiq, S. Srivathsa, and S. Dey. 2018. Pre-dispersal context and presence of opposite sex modulate density dependence and sex bias of dispersal. Oikos 127: 1596–1604.

Molina-Morales, M., J. G. Martinez, D. Martin-Galvez, and J. M. Aviles. 2012. Factors affecting natal and breeding magpie dispersal in a population parasitized by the great spotted cuckoo. Animal Behaviour 83:671–680 (erratum, Animal Behaviour 84:1082).

Morton, E. R., M. J. McGrady, I. Newton, C. J. Rollie, G. D. Smith, R. Mearns, and M. K. Oli. 2018. Dispersal: a matter of scale. Ecology 99:938–946.

Nelson, W. A., E. McCauley, and F. J. Wrona. 2001. Multiple dynamics in a single predator-prey system: experimental effects of food quality. Proceedings of the Royal Society B 268:1223–1230.

Pacala, S. W., and J. Roughgarden. 1982. Spatial heterogeneity and interspecific competition. Theoretical Population Biology 21:92–113.

Petraitis, P. S., and S. R. Dudgeon. 1999. Experimental evidence for the origin of alternative communities on rocky intertidal shores. Oikos 84:239–245.

Poethke, H. J., and T. Hovestadt. 2002. Evolution of density- and patch-size-dependent dispersal rates. Proceedings of the Royal Society B 269:637–645.

Poniatowski, D., and T. Fartmann. 2011. Dispersal capability in a habitat specialist bush cricket: the role of population density and habitat moisture. Ecological Entomology 36:717–723.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Qing, J., Z. S. Yang, K. He, Z. J. Zhang, X. D. Gu, X. Y. Yang, W. Zhang, et al. 2016. The minimum area requirements (MAR) for giant panda: an empirical study. Scientific Reports 6:37715.

Reeve, J. D., J. T. Cronin, and K. J. Haynes. 2008. Diffusion models for animals in complex landscapes: incorporating heterogeneity among substrates, individuals and edge behaviours. Journal of Animal Ecology 77:898–904.

Rivera, J. H. V, J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood Thrush post-fledging movements and habitat use in northern Virginia. Condor 100:69–78.

Rodrigues, A. M. M., and R. A. Johnstone. 2014. Evolution of positive and negative density-dependent dispersal. Proceedings of the Royal Society B 281:20141226.

Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. Ecology 81:1642–1653.

Roper, T. J., J. R. Ostler, and L. Conradt. 2003. The process of dispersal in badgers *Meles meles*. Mammal Review 33:314–318.

RStudio Team. 2016. RStudio: integrated development for R. RStudio, Boston.

Sæther, B. E., S. Engen, and R. Lande. 1999. Finite metapopulation models with density-dependent migration and stochastic local dynamics. Proceedings of the Royal Society B 266:113–118.

Saura, S., O. Bodin, and M. J. Fortin. 2014. Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. Journal of Applied Ecology 51:171–182.

Schroder, A., L. Persson, and A. M. De Roos. 2005. Direct experimental evidence for alternative stable states: a review. Oikos 110:3–19.

Schultz, C. B., and E. E. Crone. 2005. Patch size and connectivity thresholds for butterfly habitat restoration. Conservation Biology 19:887–896.

Serrano, D., D. Oro, E. Ursua, and J. L. Tella. 2005. Colony size selection determines adult survival and dispersal preferences: Allee effects in a colonial bird. American Naturalist 166:E22–E31.

Shmida, A., and S. Ellner. 1984. Coexistence of plant-species with similar niches. Vegetatio 58:29–55.

Sibly, R. M., D. Barker, M. C. Denham, J. Hone, and M. Pagel. 2005. On the regulation of populations of mammals, birds, fish, and insects. Science 309:607–610.

Simonsohn, U. 2018. Two lines: a valid alternative to the invalid testing of U-shaped relationships with quadratic regressions. Association for Psychological Science 1:538–555.

Smith, J. E., and G. O. Batzli. 2006. Dispersal and mortality of prairie voles (*Microtus ochrogaster*) in fragmented landscapes: a field experiment. Oikos 112:209–217.

Strong, D. R., and P. D. Stiling. 1983. Wing dimorphism changed by experimental density manipulation in a planthopper (*Prokelisia-marginata*, Homoptera, Delphacidae). Ecology 64:206–209.

Sugiyama, A., L. S. Comita, T. Masaki, R. Condit, and S. P. Hubbell. 2018. Resolving the paradox of clumped seed dispersal: positive density and distance dependence in a bat-dispersed species. Ecology 99:2583–2591.

Sutherland, J. P. 1990. Perturbations, resistance, and alternative views of the existence of multiple stable points in nature. American Naturalist 136:270–275.

Travis, J. M. J., D. J. Murrell, and C. Dytham. 1999. The evolution of density-dependent dispersal. Proceedings of the Royal Society B 266:1837–1842.

Turchin, P., and A. D. Taylor. 1992. Complex dynamics in ecological time-series. Ecology 73:289–305.

Van De Koppel, J., P. M. J. Herman, P. Thoolen, and C. H. R. Heip. 2001. Do alternate stable states occur in natural ecosystems? evidence from a tidal flat. Ecology 82:3449–3461.

van de Leemput, I. A., T. P. Hughes, E. H. van Nes, and M. Scheffer. 2016. Multiple feedbacks and the prevalence of alternate stable states on coral reefs. Coral Reefs 35:857–865.

Vandermeer, J., and R. Carvajal. 2001. Metapopulation dynamics and the quality of the matrix. American Naturalist 158:211–220.

Van Hooft, P., J. F. Cosson, S. Vibe-Petersen, and H. Leirs. 2008. Dispersal in *Mastomys natalensis* mice: use of fine-scale genetic analyses for pest management. Hereditas 145:262–273.

Walter, J. A., D. M. Johnson, and K. J. Haynes. 2017. Spatial variation in Allee effects influences patterns of range expansion. Ecography 40:179–188.

Wang, W. D. 2016. Population dispersal and Allee effect. Ricerche Di Matematica 65:535–548.

Wolff, J. O. 1997. Population regulation in mammals: an evolutionary perspective. Journal of Animal Ecology 66:1–13.

References Cited Only in the Online Enhancements

Aars, J., and R. A. Ims. 2000. Population dynamic and genetic consequences of spatial density-dependent dispersal in patchy populations. American Naturalist 155:252–265.

Albrectsen, B., and G. Nachman. 2001. Female-biased density-dependent dispersal of a tephritid fly in a fragmented habitat and its implications for population regulation. Oikos 94:263–272.

Alonso, J. C., E. Martin, J. A. Alonso, and M. B. Morales. 1998. Proximate and ultimate causes of natal dispersal in the great bustard *Otis tarda*. Behavioral Ecology 9:243–252.

Andreassen, H. P., and R. A. Ims. 2001. Dispersal in patchy vole populations: role of patch configuration, density dependence, and demography. Ecology 82:2911–2926.

Azandeme-Hounmalon, G. Y., S. Fellous, S. Kreiter, K. K. M. Fiaboe, S. Subramanian, M. Kungu, and T. Martin. 2014. Dispersal behavior of *Tetranychus evansi* and *T. urticae* on tomato at several spatial scales and densities: implications for integrated pest management. PLoS ONE 9:e95071.

Baguette, M., J. Clobert, and N. Schtickzelle. 2011. Metapopulation dynamics of the bog fritillary butterfly: experimental changes in habitat quality induced negative density-dependent dispersal. Ecography 34:170–176.

Bateman, A. W., A. Ozgul, T. Coulson, and T. H. Clutton-Brock. 2012. Density dependence in group dynamics of a highly social mongoose, *Suricata suricatta*. Journal of Animal Ecology 81:628–639.

Bengtsson, G., K. Hedlund, and S. Rundgren. 1994. Food-dependent and density-dependent dispersal—evidence from a soil collembolan. Journal of Animal Ecology 63:513–520.

Bengtsson, G., T. Ryden, M. S. Ohrn, and M. Wiktorsson. 2002. Statistical analysis of the influence of conspecifics on the dispersal of a soil collembola. Theoretical Population Biology 61:97–113.

Berggren, H., J. Tinnert, and A. Forsman. 2012. Spatial sorting may explain evolutionary dynamics of wing polymorphism in pygmy grasshoppers. Journal of Evolutionary Biology 25:2126–2138.

Bret, V., B. Bergerot, H. Capra, V. Gouraud, and N. Lamouroux. 2016. Influence of discharge, hydraulics, water temperature, and dispersal on density synchrony in brown trout populations (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 73:319–329.

Brooke, M. D. 2010. Vertical transmission of feather lice between adult black birds *Turdus merula* and their nestlings: a lousy perspective. Journal of Parasitology 96:1076–1080.

Broseth, H., J. Tufto, H. C. Pedersen, H. Steen, and L. Kastdalen. 2005. Dispersal patterns in a harvested willow ptarmigan population. Journal of Applied Ecology 42:453–459.

Byrom, A. E. 2002. Dispersal and survival of juvenile feral ferrets *Mustela furo* in New Zealand. Journal of Applied Ecology 39:67–78.

Callihan, J. L., C. H. Godwin, and J. A. Buckel. 2014. Effect of demography on spatial distribution: movement patterns of the Albemarle Sound-Roanoke River stock of Striped Bass (*Morone saxatilis*) in relation to their recovery. Fishery Bulletin 112:131–143.

Chaput-Bardy, A., A. Gregoire, M. Baguette, A. Pagano, and J. Secondi. 2010. Condition and phenotype-dependent dispersal in a damselfly, *Calopteryx splendens*. PLoS ONE 5:e10694.

Cote, J., S. Fogarty, T. Brodin, K. Weinersmith, and A. Sih. 2011. Personality-dependent dispersal in the invasive mosquitofish: group composition matters. Proceedings of the Royal Society B 278:1670–1678.

Crisp, D. T. 1993. Population-densities of juvenile trout (*Salmo-trutta*) in 5 upland streams and their effects upon growth, survival and dispersal. Journal of Applied Ecology 30:759–771.

Dahirel, M., A. Ansart, and L. Madec. 2014. Stage- and weather-dependent dispersal in the brown garden snail *Cornu aspersum*. Population Ecology 56:227–237.

Day, R., P. Gilmour, and S. Huchette. 2004. Effects of density and food supply on postlarval abalone: behaviour, growth and mortality. Journal of Shellfish Research 23:1009–1018.

De Meester, N., and D. Bonte. 2010. Information use and density-dependent emigration in an agrobiont spider. Behavioral Ecology 21:992–998.

De Roissart, A., E. de la Pena, L. Van Oyen, T. Van Leeuwen, D. J. Ballhorn, and D. Bonte. 2013. The presence of root-feeding nematodes—not AMF—affects an herbivore dispersal strategy. Acta Oecologica 52:38–44.

Doak, P. 2000. Population consequences of restricted dispersal for an insect herbivore in a subdivided habitat. Ecology 81:1828–1841.

Donaldson, J. R., S. W. Myers, and C. Gratton. 2007. Density-dependent responses of soybean aphid (*Aphis glycines* Matsumura) populations to generalist predators in mid to late season soybean fields. Biological Control 43:111–118.

Drolet, D., M. R. S. Coffin, M. A. Barbeau, and D. J. Hamilton. 2013. Influence of intra- and interspecific interactions on short-term movement of the amphipod *Corophium volutator* in varying environmental conditions. Estuaries and Coasts 36:940–950.

Einum, S., and K. H. Nislow. 2005. Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. Oecologia 143:203–210.

Einum, S., L. Sundt-Hansen, and K. H. Nislow. 2006. The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. Oikos 113:489–496.

Elliott, J. M. 2003. A comparative study of the dispersal of 10 species of stream invertebrates. Freshwater Biology 48:1652–1668.

Etherington, L. L., D. B. Eggleston, and W. T. Stockhausen. 2003. Partitioning loss rates of early juvenile blue crabs from seagrass habitats into mortality and emigration. Bulletin of Marine Science 72:371–391.

Fasola, M., H. Hafner, Y. Kayser, R. E. Bennetts, and F. Cezilly. 2002. Individual dispersal among colonies of Little Egrets *Egretta garzetta*. Ibis 144:192–199.

Fattebert, J., G. Balme, T. Dickerson, R. Slotow, and L. Hunter. 2015. Density-dependent natal dispersal patterns in a leopard population recovering from over-harvest. PLoS ONE 10:15.

Fonseca, D. M., and D. D. Hart. 1996. Density-dependent dispersal of black fly neonates is mediated by flow. Oikos 75:49–58.

French, D. R., and J. M. J. Travis. 2001. Density-dependent dispersal in host-parasitoid assemblages. Oikos 95:125–135.

Fronhofer, E. A., T. Kropf, and F. Altermatt. 2015. Density-dependent movement and the consequences of the Allee effect in the model organism *Tetrahymena*. Journal of Animal Ecology 84:712–722.

Hahne, J., T. Jenkins, S. Halle, and G. Heckel. 2011. Establishment success and resulting fitness consequences for vole dispersers. Oikos 120:95–105.

Hauzy, C., F. D. Hulot, A. Gins, and M. Loreau. 2007. Intra- and interspecific density-dependent dispersal in an aquatic prey-predator system. Journal of Animal Ecology 76:552–558.

Hendrickx, F., S. C. F. Palmer, and J. M. J. Travis. 2013. Ideal free distribution of fixed dispersal phenotypes in a wing dimorphic beetle in heterogeneous landscapes. Ecology 94:2487–2497.

Herzig, A. L. 1995. Effects of population-density on long-distance dispersal in the goldenrod beetle *Trirhabda-virgata*. Ecology 76:2044–2054.

Hibbard, B. E., M. L. Higdon, D. P. Duran, Y. M. Schweikert, and M. R. Ellersieck. 2004. Role of egg density on establishment and plant-to-plant movement by western corn rootworm larvae (Coleoptera: Chrysomelidae). Journal of Economic Entomology 97:871–882.

Huffeldt, N. P., I. N. Aggerholm, N. H. Brandtberg, J. H. Jorgensen, K. Dichmann, and P. Sunde. 2012. Compounding effects on nest-site dispersal of Barn Owls *Tyto alba*. Bird Study 59:175–181.

Humphries, S. 2002. Dispersal in drift-prone macroinvertebrates: a case for density-independence. Freshwater Biology 47:921–929.

Ims, R. A., and H. P. Andreassen. 2005. Density-dependent dispersal and spatial population dynamics. Proceedings of the Royal Society B 272:913–918.

Itonaga, N., U. Koppen, M. Plath, and D. Wallschlager. 2011. Declines in breeding site fidelity in an increasing population of White Storks *Ciconia ciconia*. Ibis 153:636–639.

Izraylevich, S., and U. Gerson. 1995. Sex ratio of *Hemisarcoptes coccophagus*, a mite parasitic on insects: density-dependent processes. Oikos 74:439–446.

Johnson, E. G., and D. B. Eggleston. 2010. Population density, survival and movement of blue crabs in estuarine salt marsh nurseries. Marine Ecology Progress Series 407:135–150.

Kerans, B. L., P. L. Chesson, and R. A. Stein. 2000. Assessing density-dependent establishment and dispersal: an example using caddisfly larvae. Canadian Journal of Fisheries and Aquatic Sciences 57:1190–1199.

Keynan, O., and A. R. Ridley. 2016. Component, group and demographic Allee effects in a cooperatively breeding bird species, the Arabian babbler (*Turdoides squamiceps*). Oecologia 182:153–161.

Kuefler, D., T. Avgar, and J. M. Fryxell. 2012. Rotifer population spread in relation to food, density and predation risk in an experimental system. Journal of Animal Ecology 81:323–329.

Lancaster, J., B. J. Downes, and A. Arnold. 2011. Lasting effects of maternal behaviour on the distribution of a dispersive stream insect. Journal of Animal Ecology 80:1061–1069.

Le Galliard, J. F., R. Ferriere, and J. Clobert. 2003. Mother-offspring interactions affect natal dispersal in a lizard. Proceedings of the Royal Society B 270:1163–1169.

Loe, L. E., A. Mysterud, V. Veiberg, and R. Langvatn. 2009. Negative density-dependent emigration of males in an increasing red deer population. Proceedings of the Royal Society B 276:2581–2587.

Lutz, C. L., D. R. Diefenbach, and C. S. Rosenberry. 2015. Population density influences dispersal in female white-tailed deer. Journal of Mammalogy 96:494–501.

Mabry, K. E. 2014. Effects of sex and population density on dispersal and spatial genetic structure in brush mice. Journal of Mammalogy 95:981–991.

Manteuffel, V. M., and M. Eiblmaier. 2010. Density-dependent processes during the juvenile stage in the lizard *Sceloporus virgatus*. Journal of Herpetology 44:21–27.

Martin, C. A., J. C. Alonso, J. A. Alonso, C. Palacin, M. Magana, and B. Martin. 2008. Natal dispersal in great bustards: the effect of sex, local population size and spatial isolation. Journal of Animal Ecology 77:326–334.

Mathieu, J., S. Barot, M. Blouin, G. Caro, T. Decaens, F. Dubs, L. Dupont, et al. 2010. Habitat quality, conspecific density, and habitat pre-use affect the dispersal behaviour of two earthworm species, *Aporrectodea icterica* and *Dendrobaena veneta*, in a mesocosm experiment. Soil Biology and Biochemistry 42:203–209.

McKellar, A. E., M. W. Reudink, P. P. Marra, L. M. Ratcliffe, and S. Wilson. 2015. Climate and density influence annual survival and movement in a migratory songbird. Ecology and Evolution 5:S892–S904.

Meylan, S., J. Clobert, and B. Sinervo. 2007. Adaptive significance of maternal induction of density-dependent phenotypes. Oikos 116:650–661.

Michler, S. P. M., M. Nicolaus, R. Ubels, M. van der Velde, C. Both, J. M. Tinbergen, and J. Komdeur. 2011. Do sex-specific densities affect local survival of free-ranging great tits? Behavioral Ecology 22:869–879.

Midtgaard, F. 1999. Is dispersal density-dependent in carabid beetles? a field experiment with *Harpalus rufipes* (Degeer) and *Pterostichus niger* (Schaller) (Col., Carabidae). Journal of Applied Entomology 123:9–12.

Moksnes, P. O. 2004. Interference competition for space in nursery habitats: density-dependent effects on growth and dispersal in juvenile shore crabs *Carcinus maenas*. Marine Ecology Progress Series 281:181–191.

Newton, I. 2001. Causes and consequences of breeding dispersal in the Sparrowhawk *Accipiter nisus*. Ardea 89:143–154.

Nowicki, P., and V. Vrabec. 2011. Evidence for positive density-dependent emigration in butterfly metapopulations. Oecologia 167:657–665.

Ost, M., A. Lehikoinen, K. Jaatinen, and M. Kilpi. 2011. Causes and consequences of fine-scale breeding dispersal in a female-philopatric species. Oecologia 166:327–336.

Overholtzer-McLeod, K. L. 2004. Variance in reef spatial structure masks density dependence in Coral-Reef fish populations on natural versus artificial reefs. Marine Ecology Progress Series 276:269–280.

Paris, D., A. O. Nicholls, A. Hall, A. Harvey, and M. Massaro. 2016. Female-biased dispersal in a spatially restricted endemic island bird. Behavioral Ecology and Sociobiology 70:2061–2069.

Pasinelli, G., and J. R. Walters. 2002. Social and environmental factors affect natal dispersal and philopatry of male red-cockaded woodpeckers. Ecology 83:2229–2239.

Payne, R. B. 1991. Natal dispersal and population-structure in a migratory songbird, the indigo bunting. Evolution 45:49–62.

Pennekamp, F., K. A. Mitchell, A. Chaine, and N. Schtickzelle. 2014. Dispersal propensity in *Tetrahymena thermophila* ciliates—a reaction norm perspective. Evolution 68:2319–2330.

Powers, S. P., and C. H. Peterson. 2000. Conditional density dependence: the flow trigger to expression of density-dependent emigration in bay scallops. Limnology and Oceanography 45:727–732.

Randall, J. A., K. Rogovin, P. G. Parker, and J. A. Eimes. 2005. Flexible social structure of a desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints. Behavioral Ecology 16:961–973.

Rasmussen, J. E., and M. C. Belk. 2012. Dispersal behavior correlates with personality of a North American fish. Current Zoology 58:260–270.

Reyns, N. B., and D. B. Eggleston. 2004. Environmentally-controlled, density-dependent secondary dispersal in a local estuarine crab population. Oecologia 140:280–288.

Rhainds, M., G. Gries, C. T. Ho, and P. S. Chew. 2002. Dispersal by bagworm larvae, *Metisa plana*: effects of population density, larval sex, and host plant attributes. Ecological Entomology 27:204–212.

Rhainds, M., and R. H. Messing. 2005. Spatial and temporal density dependence in a population of melon aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), on established and sentinel taro plants. Applied Entomology and Zoology 40:273–282.

Rhainds, M., L. Shipp, L. Woodrow, and D. Anderson. 2005. Density, dispersal, and feeding impact of western flower thrips (Thysanoptera: Thripidae) on flowering chrysanthemum at different spatial scales. Ecological Entomology 30:96–104.

Richardson, K., J. G. Ewen, D. P. Armstrong, and M. E. Hauber. 2010. Sex-specific shifts in natal dispersal dynamics in a reintroduced hihi population. Behaviour 147:1517–1532.

Ronnas, C., A. Cassel-Lundhagen, A. Battisti, J. Wallen, and S. Larsson. 2011. Limited emigration from an outbreak of a forest pest insect. Molecular Ecology 20:4606–4617.

Rosenberg, R., H. C. Nilsson, K. Hollertz, and B. Hellman. 1997. Density-dependent migration in an *Amphiura filiformis* (Amphiuridae, Echinodermata) infaunal population. Marine Ecology Progress Series 159:121–131.

Rouquette, J. R., and D. J. Thompson. 2007. Patterns of movement and dispersal in an endangered damselfly and the consequences for its management. Journal of Applied Ecology 44:692–701.

Roy, J., G. Yannic, S. D. Cote, and L. Bernatchez. 2012. Negative density-dependent dispersal in the American black bear (*Ursus americanus*) revealed by noninvasive sampling and genotyping. Ecology and Evolution 2:525–537.

Sandeson, P. D., G. Boiteau, and J. P. R. Le Blanc. 2002. Adult density and the rate of Colorado potato beetle (Coleoptera: Chrysomelidae) flight take-off. Environmental Entomology 31:533–537.

———. 2004. Effect of adult Colorado potato beetle density on dispersal under field conditions. Environmental Entomology 33:1421–1430.

Santoro, S., A. J. Green, and J. Figuerola. 2013. Environmental instability as a motor for dispersal: a case study from a growing population of glossy ibis. PLoS ONE 8:12.

Scandolara, C., R. Lardelli, G. Sgarbi, M. Caprioli, R. Ambrosini, D. Rubolini, and N. Saino. 2014. Context-, phenotype-, and kin-dependent natal dispersal of barn swallows (*Hirundo rustica*). Behavioral Ecology 25:180–190.

Schulz, U. H., and M. E. Leal. 2012. Effects of stocking density on dispersal behavior of Brazilian freshwater dourado (*Salminus brasiliensis*) in a subtropical river headwater. Neotropical Ichthyology 10:409–415.

Stasek, D. J., J. N. Radl, and T. O. Crist. 2018. The effects of dispersal and predator density on prey survival in an insect-red clover metacommunity. Journal of Insect Science 18, https://doi.org/10.1093/jisesa/iex100.

Stauffer, G. E., J. J. Rotella, R. A. Garrott, and W. L. Kendall. 2014. Environmental correlates of temporary emigration for female

Weddell seals and consequences for recruitment. Ecology 95:2526–2536.

Stoen, O. G., A. Zedrosser, S. Saebo, and J. E. Swenson. 2006. Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. Oecologia 148:356–364.

Strevens, C. M. J., and M. B. Bonsall. 2011. Density-dependent population dynamics and dispersal in heterogeneous metapopulations. Journal of Animal Ecology 80:282–293.

Tatara, C. P., S. C. Riley, and B. A. Berejikian. 2011. Effects of hatchery fish density on emigration, growth, survival, and predation risk of natural steelhead parr in an experimental stream channel. North American Journal of Fisheries Management 31:224–235.

Tripet, F., A. Jacot, and H. Richner. 2002. Larval competition affects the life histories and dispersal behavior of an avian ectoparasite. Ecology 83:935–945.

Van Allen, B. G., and P. Bhavsar. 2014. Natal habitat effects drive density-dependent scaling of dispersal decisions. Oikos 123:699–704.

Ventura, L., D. R. Smith, and Y. Lubin. 2017. Crowding leads to fitness benefits and reduced dispersal in a colonial spider. Behavioral Ecology 28:1384–1392.

Waser, P. M., J. D. Busch, C. R. McCormick, and J. A. DeWoody. 2006. Parentage analysis detects cryptic precapture dispersal in a philopatric rodent. Molecular Ecology 15:1929–1937.

Wauters, L. A., E. Matthysen, F. Adriaensen, and G. Tosi. 2004. Within-sex density dependence and population dynamics of red squirrels *Sciurus vulgaris*. Journal of Animal Ecology 73:11–25.

Westerberg, L., T. Lindstrom, E. Nilsson, and U. Wennergren. 2008. The effect on dispersal from complex correlations in small-scale movement. Ecological Modelling 213:263–272.

Wojan, C. M., S. M. Knapp, and K. E. Mabry. 2015. Spatial variation in population density affects dispersal behavior in brush mice. Ecology 96:1661–1669.

Zavorka, L., D. Aldven, J. Naslund, J. Hojesjo, and J. I. Johnsson. 2015. Linking lab activity with growth and movement in the wild: explaining pace-of-life in a trout stream. Behavioral Ecology 26:877–884.

Associate Editor: Jeremy W. Fox
Editor: Alice A. Winn

“These favored regions, besides those of the Aru Islands, where birds of paradise also abound, are rich in vegetation beyond even the usual fecundity of the tropics. Almost as unique, varied and lovely, are other forms of animal life—butterflies, dragon-flies, lizards, insects great and small, and countless tribes of the feathered race.” Figured: “*Seleucides alba*.” From “Some Birds of Paradise from New Guinea” by Geo. S. Mead (*The American Naturalist*, 1894, 28:915–920).