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Finite metapopulation models with density-dependent migration and stochastic local dynamics

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The effects of small density-dependent migration on the dynamics of a metapopulation are studied in a model with stochastic local dynamics. We use a diffusion approximation to study how changes in the migration rate and habitat occupancy affect the rates of local colonization and extinction. If the emigration rate increases or if the immigration rate decreases with local population size, a positive expected rate of change in habitat occupancy is found for a greater range of habitat occupancies than when the migration is density-independent. In contrast, the reverse patterns of density dependence in respective emigration and immigration reduce the range of habitat occupancies where the metapopulation will be viable. This occurs because density-dependent migration strongly influences both the establishment and rescue effects in the local dynamics of metapopulations.

Keywords: metapopulation models; density-dependent migration; risk of extinction; stochastic population dynamics; establishment and rescue effects

1. INTRODUCTION

Analyses of Levins-type metapopulation models have shown that, for a metapopulation to persist, the colonization rate must be larger than the extinction rate of local patches (Levins 1970; Hanski 1997). At equilibrium, the fraction of occupied patches will decrease when the colonization rate decreases relative to the extinction rate. Such strong effects of migration were also found in models including both local dynamics as well as demographic and environmental stochasticity (Lande *et al.* 1998).

A fundamental assumption made in most stochastic and deterministic models of metapopulation dynamics is that the migration rate is independent of the local population size. In fact, there is no significant relationship between migration rate and population size in many species of vertebrates (Gaines & McClenagh 1980). However, empirical evidence also shows that population density may affect the rate of migration, especially the natal dispersal rate (Wolff 1997). Two different patterns of density-dependent dispersal rates have been recorded. First, dispersal rate may be positively density-dependent, i.e. the probability that an individual emigrates increases with local population size. This pattern has been documented in several species of birds (e.g. Watson *et al.* 1984; Nilsson 1989; Veit & Lewis 1996) as well as mammals (e.g. Berger 1987; Krebs 1992; Sinclair 1992). Density-dependent increase in dispersal, often involving development of particular morphological forms, also occurs in many insect species from the orders Thysanoptera, Homoptera and Heteroptera (Denno & Peterson 1995). Second, the dispersal rate may decrease with increasing density. Such a negative density-dependent relationship has especially been recorded in many territorial mammalian species (see examples in Wolff 1997; Diffendorfer 1998; Diffendorfer *et al.* 1999), but has been recorded in other taxa as well (e.g. Doncaster *et al.* 1997).

Population density may not only affect the dispersal rate. Although much less empirical information is available, population size may also affect the immigration rate (Ray *et al.* 1991). It has been suggested that the number of conspecifics present can be used as an indicator of the quality of the area (Kiester & Slatkin 1974; Kiester 1979; Danchin *et al.* 1991; Stamps 1991). For instance, in many colonial bird species with an active nest defence, higher reproductive success is found in larger colonies than in smaller colonies (Wiklund & Andersson 1980), which may favour aggregation of individuals into larger units. However, in many colonial seabird species, immigration rate decreases with increasing population size (Duncan 1978; Porter & Coulson 1987; Coulson 1991), which is often due to difficulties in obtaining favourable breeding sites at high densities (Birkhead & Furness 1985; Croxall & Rothery 1991). Such a density-dependent decrease in immigration rate is also found in many solitary species (e.g. Danielson & Gaines 1987; Doncaster *et al.* 1997).

Here we will examine the effects of density-dependent dispersal and immigration in a finite metapopulation model (Lande *et al.* 1998) that includes both local dynamics and environmental stochasticty. We thus avoid making the simplifying assumptions about a constant

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extinction and colonization rate that is commonly made in extensions of Levins-type metapopulation models (Gyllenberg *et al.* 1997). Hence, we can study how various forms of density-dependent migration rates affect local population dynamics and determine extinction and colonization of the subpopulations.

2. THE MODEL

We consider a classical, closed metapopulation with n identical suitable habitat patches that are assumed to be either occupied or not occupied by the species. As a consequence of the stochastic local population dynamics described below, successful colonization of an unoccupied patch and local extinction occur randomly in time as Poisson processes. Following Lande *et al.* (1998), a close approximation for the mean time to metapopulation extinction can be obtained by applying diffusion theory (Karlin & Taylor 1981) to both the local and global dynamics, assuming low rates of colonization and local extinction. The expected rate of change of habitat occupancy or the infinitesimal mean of the diffusion for the proportion of patches occupied, p, is

$$\mu(p) = c(p)p(1-p) - e(p)p, \tag{1}$$

where $c(p)$ is the colonization rate and $e(p)$ is the extinction rate. The variance per unit time in the rate of change of habitat occupancy, the infinitesimal variance of the diffusion process for p, is

$$\sigma^2(p) = \frac{c(p)p(1-p) + e(p)p}{n}. \tag{2}$$

Consider a metapopulation of n local populations with similar demographic parameters and independent environmental stochasticity. Extinction and colonization of a patch must be dependent on the habitat occupancy through the effects of immigration from other occupied patches. We define a successful colonization to occur when a local population founded from a single immigrant first reaches the mean size for the current habitat occupancy, $\bar{N}_{+(p)}$ and for each new migrant to an unoccupied patch the probability of this event is denoted $u(1,p)$. Assuming a constant rate of emigration per individual, m, the rate of successful colonization is

$$c(p) = m\bar{N}_{+}u(1,p), \tag{3}$$

where $m\bar{N}_{+}$ is the expected number of emigrants from an occupied patch.

After the local population has reached the mean size for the current habitat occupancy, the mean to local extinction (reaching zero individuals) is $T(\bar{N}_{+},p)$. The local extinction rate is the inverse of the mean time to local extinction,

$$e(p) = 1/T(\bar{N}_{+},p). \tag{4}$$

(a) *Density-dependent emigration*

The colonization rate $(c(p))$, the extinction rate $(e(p))$ and the occupancy rate $(\mu(p))$ can be calculated by modelling the local population dynamics. In the case of no migration we assume that the dynamics of the local population can be approximated by a diffusion with infinitesimal mean and variance, $f(N)$ and $\nu(N)$, respectively. Migration will, however, strongly influence the local dynamics. We assume that individuals emigrate from island i at a density-dependent rate

$$m_\theta = m_0 + \theta(N_i - N^*), \tag{5}$$

where $N^* = \bar{N}_{+}(p^*)$ and p^* is the stable equilibrium value of the habitat occupancy p. Hence, m_0 is by definition the emigration rate for populations of size N^*. This is equivalent to assuming that each population of size N^* has the same rate of migration m_0, regardless of the value of θ. Such a standardization is necessary to compare the effects of differences in the density-dependent migration rate, because we wish to prevent that variation in the absolute number of migrants affects the comparisons. Positive values of θ represent a linear increase in the rate of emigration with increasing population size, whereas $\theta < 0$ represents a density-dependent decrease in emigration rate. The emigrating individuals are assumed to distribute themselves at random among the n suitable patches.

Assuming no mortality during the migration, it is shown in Appendix A that with a small migration rate per individual per unit time, the diffusion approximation for the local population size N has infinitesimal mean and variance

$$M(N) = f(N) - m_\theta N + m_0 p\bar{N}_{+} + \theta pH, \tag{6a}$$

$$V(N) = \nu(N) + m_\theta N + m_0 p\bar{N}_{+} + \theta pH, \tag{6b}$$

where $H = \mathrm{E}[(N - N^*)N] = \sigma^2_{N_+} + \bar{N}_{+}(\bar{N}_{+} - N^*)$. Here $\sigma^2_{N_+}$ is the variance in population size of occupied patches, and $f(N)$ and $\nu(N)$ are the infinitesimal mean and variance of the local dynamics without migration. The interpretation of $M(N)$ and $V(N)$ is that the expectation and the variance of for small or moderate changes in population size during a small time Δt is $M(N)\Delta t$ and $V(N)\Delta t$, respectively.

Based on the results from diffusion theory (Karlin & Taylor 1981; Lande 1993), the mean time to extinction starting from $\bar{N}_{+}$ can be derived as

$$T(\bar{N}_{+},p) = \int_0^\infty G(N,\bar{N}_{+})\mathrm{d}N, \tag{7a}$$

where

$$G(N,N_0) = \begin{cases} \dfrac{2}{V(N)s(N)}\displaystyle\int_0^N s(x)\mathrm{d}x \text{ for } N < N_0 \\ \dfrac{2}{V(N)s(N)}\displaystyle\int_0^{N_0} s(x)\mathrm{d}x \text{ for } N \geqslant N_0 \end{cases} \tag{7b}$$

is the Green function (the probability distribution of time spent at each population size before extinction starting at N_0), and $s(x) = \exp\{-2\int^x (M(N)/V(N))\mathrm{d}N\}$. From the quasi-stationary distribution $G(N,\bar{N}_{+})/T(\bar{N}_{+},p)$ we can calculate the mean size of occupied populations before extinction

$$\bar{N}_{+} = \int_0^\infty N\frac{G(N;\bar{N}_{+})}{T(\bar{N}_{+},p)}\mathrm{d}N. \tag{8}$$

(b) *Density-dependent immigration*

Now assume that individuals emigrate at a constant rate m_0 from the occupied islands into a pool of emigrants, that then distribute themselves according to relative size of the recipient populations. The probability that a migrating individual immigrates to an island with $\mathcal{N}$ individuals is $[m_0 + \theta(\mathcal{N} - p\bar{\mathcal{N}}_+)]/[m_0 n]$ where $\theta < m_0/K$. If $\theta > 0$ the probability of immigration will increase with population size, whereas $\theta < 0$ represents a decrease in the probability of immigration with increasing population size. This gives the diffusion approximation with infinitesimal mean and variance (see Appendix A)

$$M(\mathcal{N}) = f(\mathcal{N}) - (m_0 - \theta p\bar{\mathcal{N}}_+)(\mathcal{N} - p\bar{\mathcal{N}}_+), \qquad (9a)$$

$$V(\mathcal{N}) = \nu(\mathcal{N}) + m_0\mathcal{N} + m_\theta p\bar{\mathcal{N}}_+. \qquad (9b)$$

3. RESULTS

As in the case of a constant migration rate (Lande *et al.* 1998), two positive equilibria of habitat occupancy (given by the solution to $\mu = 0$) exist for certain parameter values when there is density-dependent emigration (figure 1*a*) or immigration (figure 2*a*). The higher equilibrium is stable, whereas the lower one is unstable.

When the emigration rate increases with local population size ($\theta > 0$), the stable equilibrium occurs at a larger occupancy rate, p, than for a negative density dependence in the emigration rate (figure 1*a*). Similarly, the lower (unstable) equilibrium occurs at a smaller p when the emigration rate increases with population size, compared to the equilibrium that is found when the emigration rate is either density-independent or negative density-dependent. Consequently, the expected rate of change in habitat occupancy is positive for a greater range of values of p when the emigration rate increases with population size compared to the case of negative density-dependent emigration. This is due to a higher colonization rate, for a given p, when there is positive density-dependent emigration (figure 1*b*). In addition, for larger p, the extinction rate is also lower (figure 1*c*). However, when few patches are occupied, local extinction rate is higher for positive than for negative density-dependence because the emigration rate becomes very low.

When density-dependence is introduced in the immigration rate, assuming density-independent emigration into a common pool of potential recruits, a strong effect on the local dynamics appears. When immigration rate decreases with increasing population size ($\theta < 0$), a positive expected rate of change in habitat occupancy is found for a greater range of values of p than when the immigration rate is constant or increases with density (figure 2*a*). This occurs because the colonization rate is higher (figure 2*b*) and the extinction rate (figure 2*c*) is lower when the immigration decreases with increasing population size than when the immigration rate is density-independent or negatively density-dependent. Such an increase in extinction rate and decrease in colonization rate by conspecific attraction have previously been noted by Ray *et al.* (1991).

4. DISCUSSION

A Levins-type metapopulation model (Levins 1969, 1970) is based on assumptions that are never fulfilled in free-living population, i.e. a stable environment, patches of equal size, no local dynamics, and constant rates of migration and local extinction and colonization (Hanski 1997). Relaxing these assumptions by allowing rates of local extinction and colonization to depend on habitat occupancy creates multiple equilibria for habitat occupancy (Hanski & Gyllenberg 1993), with an unstable equilibrium at low habitat occupancy corresponding to an Allee-effect at the metapopulation level. Similar results were obtained when local dynamics and environmental stochasticity were introduced into such a Levins-type-model (Lande *et al.* 1998), even though the time to extinction was much longer than in a classical metapopulation model. Here we have shown (figures 1*a* and 2*a*) that

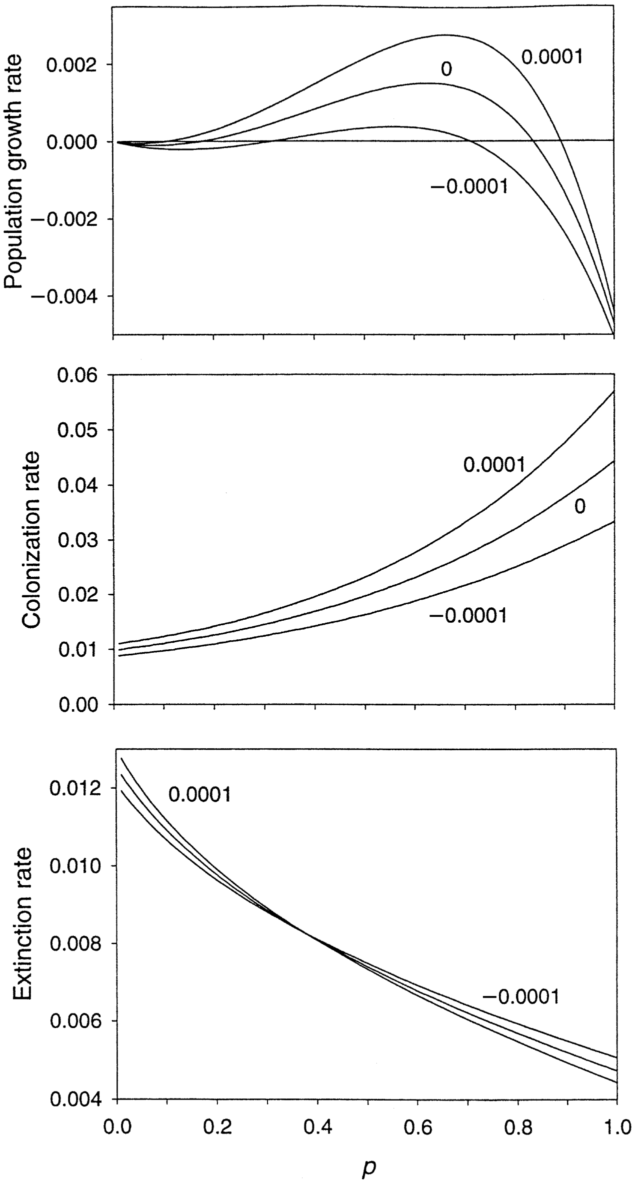

Figure 1. (*a*) The expected rate of change in habitat occupancy, $\mu(p)$, (*b*) the colonization rate, $c(p)$ and (*c*) the extinction rate, $e(p)$ as functions of habitat occupancy p for different density-dependence in the emigration rate, θ. Positive values of θ represent an increasing emigration rate with population size whereas the emigration rate decreases with population size when $\theta < 0$. Density-independent emigration corresponds to $\theta = 0$. Expected local dynamics are logistic with carrying capacity $K = 50$, mean intrinsic rate of increase $r = 0.01$, demographic and environmental variance $\sigma_d^2 = 1$ and $\sigma_e^2 = 0.01$, and migration rate $m_0 = 0.006$.

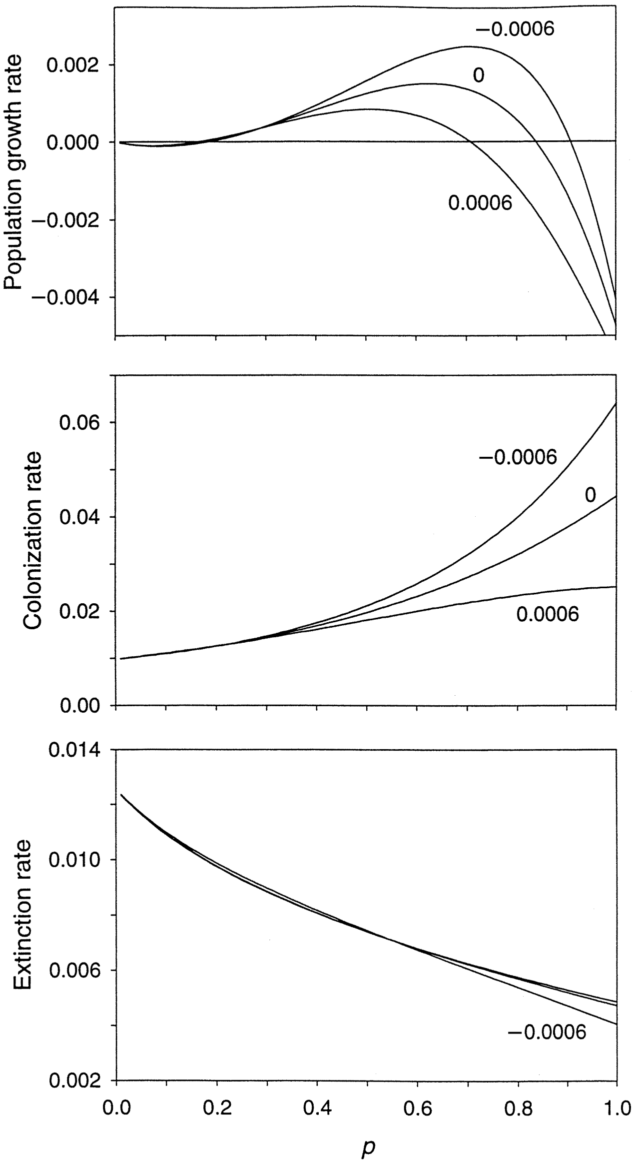

Figure 2. (*a*) The expected rate of change in habitat occupancy, $\mu(p)$, (*b*) the colonization rate, $c(p)$ and (*c*) the extinction rate, $e(p)$ as functions of habitat occupancy p for different density-dependence in the immigration rate, θ. Positive values of θ represent an increasing immigration rate with population size whereas the immigration rate decreases with population size when $\theta < 0$. Density-independent immigration corresponds to $\theta = 0$. For parameters, see figure 1.

multiple equilibria for habitat occupancy may be present in such a model also when the assumption of a constant migration rate is relaxed. This occurs because, assuming small migration rates $m \ll 1$, a large number of patches ($n \gg 2$) and no spatial autocorrelation in the environmental stochasticity, local extinction and colonization events occur for a given habitat occupancy almost independently in the different patches, justifying the use of a one-dimensional diffusion approximation to study the local dynamics. This leads to a density-dependent birth-and-death process describing the changes in the habitat-occupancy of the metapopulation, coupled with local dynamics (cf. Drechsler & Wissel 1997).

The form of the relationship between the migration rate and population size strongly affect the metapopulation dynamics (figures 1*a* and 2*a*). When the probability that an individual emigrates increases with population size, a positive rate of change in habitat occupancy is found for a greater range of habitat occupancies than for a constant migration rate. A similar effect occurs also when the immigration rate into a patch decreases with population size. In contrast, a decrease in emigration or an increase in immigration with population size reduces the rate of change in habitat occupancy, resulting in a small range of habitat occupancies where the metapopulation will be viable. The locations of these equilibria will, however, depend on the environmental variance and population growth rate. In general, the position of the stable equilibrium increases with increasing r and decreasing environmental stochasticity (Lande *et al.* 1998).

The relationship between metapopulation dynamics and the form of the density-dependence in the migration rates depends on two characteristics of metapopulation dynamics. Increasing habitat occupancy can lead to a decrease in the rate of local extinction ('the rescue effect'; Brown & Kodric-Brown 1977) or to an increase in the rate of successful colonization per migrant ('the establishment effect'; Lande *et al.* 1998). In the present model, both are manifestations of a strong coupling between local and metapopulation dynamics. Density-dependence in the migration rate strongly affects this coupling because it influences the relationship between habitat occupancy and the local dynamics. In particular, the colonization rate is strongly reduced when the emigration rate decreases (figure 1*b*) or, in particular, when the immigration rate increases (figure 2*b*) with population size (see also Ray *et al.* 1991). In addition, at high levels of habitat occupancy, a negative density-dependence either in the emigration or in the immigration rate also reduces the risk of local extinction (figures 1*c* and 2*c*). Thus, density-dependent migration may introduce a strong reinforcement of the establishment effect, as well as the rescue effect in the dynamics of metapopulations.

Our analyses have shown that, at least for small migration rates per individual and low levels of density-dependence, the relationship between migration rate and population size will strongly affect the dynamics of metapopulations. In vertebrates, some evidence suggests that dispersal is positively density-dependent in non-territorial species and negatively density-dependent in territorial species (Wolff 1997). If there is such a relationship between social system and pattern of density-dependent dispersal, our results (figures 1 and 2) suggest that detailed understanding of behavioural mechanisms determining animal migration patterns may be extremely important to obtain reliable predictions of metapopulation viability for many species.

APPENDIX A

With density-dependent emigration, the numbers of migrants from each patch are assumed to be approximately Poisson distributed with means $m_\theta N$, where $m_\theta = m_0 + \theta[N - \bar{N}_+(p^*)]$. When the immigrants are randomly distributed among the islands the number of immigrants are approximately Poisson distributed with means $1/n \Sigma m_\theta N$, where the summation is over all local populations. The covariances between the changes in population sizes due to migration can be ignored (see

Lande *et al.* 1998). Hence the component of $\Delta\mathcal{N}$ due to migration has mean

$$\mathrm{E}[\Delta\mathcal{N}] = -m_\theta\mathcal{N} + \frac{1}{n}\sum m_\theta\mathcal{N},$$

which, inserting m_θ, can be written as

$$\mathrm{E}[\Delta\mathcal{N}] \approx -m_0\mathcal{N} + m_0 p\overline{\mathcal{N}}_+ + \theta pH,$$

where

$$H = \mathrm{E}[(\mathcal{N} - \mathcal{N}^*)\mathcal{N}] = \sigma^2_{\mathcal{N}_+} + \overline{\mathcal{N}}_+(\overline{\mathcal{N}}_+ - \mathcal{N}^*).$$

The variance of the components due to migration is

$$\mathrm{var}[\Delta\mathcal{N}] = m_\theta\mathcal{N} + \frac{1}{n}\sum m_\theta\mathcal{N} \approx m_0\mathcal{N} + m_0 p\overline{\mathcal{N}}_+ + \theta pH.$$

For the model with density-dependent immigration the numbers of migrants from each island are Poisson variates with means $m_0\mathcal{N}$. The expected size of the total migrant pool is $m_0 np\overline{\mathcal{N}}_+$. The numbers of immigrants are then approximately Poisson distributed with means

$$m_0 np\overline{\mathcal{N}}_+ \frac{m_0 + \theta(\mathcal{N} - p\overline{\mathcal{N}}_+)}{nm_0} = p\overline{\mathcal{N}}_+[m_0 + \theta(\mathcal{N} - p\overline{\mathcal{N}}_+)],$$

giving the contributions to the mean and variances due to migration

$$\mathrm{E}[\Delta\mathcal{N}] = -m_0\mathcal{N} + m_\theta p\overline{\mathcal{N}}_+ = -(m_0 - \theta p\overline{\mathcal{N}}_+)(\mathcal{N} - p\mathcal{N}_+),$$

and

$$\begin{aligned}\mathrm{var}[\Delta\mathcal{N}] = m_0\mathcal{N} + m_\theta p\overline{\mathcal{N}}_+ = m_0(\mathcal{N} + p\overline{\mathcal{N}}_+) \\ + \theta p\overline{\mathcal{N}}_+(\mathcal{N} - p\overline{\mathcal{N}}_+).\end{aligned}$$

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