

Resource distribution drives the adoption of migratory, partially migratory, or residential strategies

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Abstract Organismal movement can take on a variety of spatial and temporal forms. These forms depend in part on the type and scale of environment experienced as well as the internal state of the individual. However, individuals experiencing seemingly the same environment on the same time scale can display different movement strategies. While theorists have mathematically analyzed patch models and simulated spatially-explicit models, few studies have provided a mathematical analysis of migration in spatially-explicit models. Here, we consider a spatially explicit one-dimensional model where movement is costly and individuals must return to a common breeding ground annually to reproduce. We derive the optimal movement strategy, given specific movement costs and environmental resource distributions, obtaining closed-form solutions and results in several important special cases. We find, intuitively, that steep resource clines favor migratory behavior and shallow resource clines favor residential behavior, while lower movement efficiencies and shorter breeding cycles favor residency. However, we also show that when

resource clines are sharp, migrants and residents can coinvade with each exploiting a locally optimal behavior. This can be interpreted as an example of partial migration (if migrants and residents are members of the same species). Alternatively, this can also be interpreted as two recently divergent species coinventing on a single resource, using different movement strategies to share the niche. We conclude with a discussion of density-dependent pressures on movement, including local resource depletion, and show that the density-independent results are relevant to density-dependent situations by calculating some stable strategy allocations analogous to ideal free distributions.

Keywords Partial migration · Optimal control · Coexistence

Introduction

Movement is ubiquitous among living organisms (particularly animals) and is vital for the long-term persistence and survival of any population (Hanski 1999). A large diversity of movement patterns is found in nature, spanning a range of temporal and spatial scales. These can vary from, e.g., foraging movements of nematodes *Caenorhabditis elegans* on the scale of minutes and centimeters (Pierce-Shimomura et al. 1999) to, e.g., migrations of Arctic terns (*Sterna paradisaea*) which travel almost from pole to pole and back again over the course of a year (Egevang et al. 2010). At its core, movement is an individual behavior (Kennedy 1985) and can be thought of as an adaptive response to conditions, both external and internal (Cresswell et al. 2011; Clobert et al. 2012). Intuitively, different movement strategies can be favored by different environments, by the same environment experienced on

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different scales, or by individuals with different motilities or internal states. However, particularly intriguing are cases where the same environment experienced by similar individuals on similar scales appears to select for different movement strategies.

One common example of coexistence of movement patterns is partial migration where some individuals in a population migrate in a given season while others do not (Lundberg 1988). Partial migrations can be clustered among three distinct types (Shaw and Levin 2011): non-breeding partial migration where migrants and non-migrants breed together but spend the non-breeding (e.g., winter) season apart; breeding partial migration where migrants and non-migrants spend the non-breeding season together and breed apart; and skipped-breeding partial migration where individuals must migrate to breed and non-migrants do not breed that year (Chapman et al. 2011; see Fig. 1 in Shaw and Levin 2011). In the case of skipped-breeding partial migration, individuals that do not migrate can potentially accumulate extra energy to spend on reproduction in future years (Shaw and Levin 2011, 2013). In this case, migrating and non-migrating individuals may differ in their level of energy stores (e.g., Thorpe 1994; Caut et al. 2008)—thus, the coexistence of different movement strategies can be accounted for by individuals differing in internal state.

However, the cause of coexistence between migrant and non-migrant individuals in the cases of non-breeding and breeding partial migration is less clear. The first theoretical explanations of partial migration relied on uncertainty in survival during the non-breeding period to explain the coexistence of migrant and non-migrant types (Cohen 1967; Lundberg 1987). Kaitala et al. (1993) demonstrated theoretically that non-breeding partial migrations could be maintained by separate density-dependent regulation of migrant and non-migrant types during the non-breeding season, without invoking environmental uncertainty. More recent models have focused on the combinations of density-dependent, density-independent, and stochastic factors in maintaining partial migration (Griswold et al. 2010; Vélez-Espino et al. 2013). In the case of breeding partial migrations, Taylor and Norris (2007) determined that density-dependence during the non-shared season is necessary for the coexistence of migrant and non-migrant types. Fryxell and Holt (2013) demonstrated in a general model that if two habitats can each sustain a resident population, then a population that migrates between the two habitats should be able to coexist with the resident types.

All of these models of partial migration include space only implicitly. Since migration is fundamentally an adaptive response to spatially distributed resources (Cresswell et al. 2011), spatially explicit models may provide insights that spatially implicit ones cannot. The

analysis of patch models has shown that conditional dispersal between reproductive patches can enable coexistence without niche segregation (McPeck and Holt 1992) even though unconditional dispersal between reproductive patches cannot, even in the presence of spatial heterogeneity (Hastings 1983). However, these patch models and existing partial migration models also only indirectly consider ecological conditions as experienced through survival. Migration appears to be picked up and dropped over short evolutionary time scales suggesting that current populations are migrant or resident based on existing (or recent) ecological conditions (Alerstam et al. 2003). Therefore, by explicitly considering the ecological conditions that individuals face (rather than indirect effects through survival), we may gain a deeper understanding of the conditions favoring migrant and non-migrant strategies and potentially how changes in conditions may favor switches in strategies adopted by individuals. Although spatial simulation studies of migration often explicitly include ecological conditions (e.g., Hubbard et al. 2004; Holdo et al. 2009; Shaw and Couzin 2013), they typically have not focused on questions of partial migration or coexistence of migration strategies.

In a number of species, adults feed in one habitat and migrate to a separate habitat periodically to reproduce. For example, marine turtles and seabirds forage in the open ocean and migrate to terrestrial sites for breeding, land crabs and amphibians return to water to breed, and diadromous fish and invertebrates migrate between fresh and salt water (Dingle 2014). In this paper, we construct a model for migration in such species, assuming a seasonal (time-independent) environment. In a recent paper (Reluga and Shaw 2014), we described how the tendency of some species to migrate can be understood in a spatially explicit density-independent setting as fitness optimization balancing movement costs with foraging success on a single resource. However, that analysis was limited mostly to numerical results. The model system we develop here is simple enough that we can obtain exact closed-form solutions, but has just enough temporal dependence to provide insight into competition between migration and residency. We find that some ecological conditions favor migration, others favor residency, and a subset of conditions support coinvasion by both resident and migratory strategies. This scenario illustrates how seasonal constraints on life history and in combination with costly movement can bifurcate the niche space, allowing for the potential coexistence of resident and migratory subpopulations (partial migration) or the coexistence of two species with different movement strategies, on a single resource. We conclude with a consideration of density-dependent effects. These results provide further evidence that partial migrations can evolve under local density dependence even without environmental variation.

Model

In an idealized evolutionary model of migration, we look at the case where an individual's fitness is determined by her foraging success over a lifetime, minus energy expenditures. Consider a semelparous species in a 1-dimensional habitat with a shared breeding ground at location $x = 0$ and feeding grounds for $x \geq 0$. Adults can forage anywhere, but are obligated to return to the breeding ground every year (or more generally, every T time units) to reproduce. Between breeding events, an individual may die with mortality risk δ per unit time, independent of location, behavior, state, or time of year. When forage abundance is described by a distribution $\psi(x)$ in space, and the rate of energy expenditure depends only on the speed of movement, represented by $\gamma(\dot{x})$ where \dot{x} is the individual's velocity, then the fitness of an individual moving along a path $x(t)$ over its lifetime, with $x(0) = x(T) = 0$, can be represented by the discounted reproductive value

$$\mathcal{R}_d := \max \left\{ 0, e^{-\delta T} \int_0^T \psi(x(t)) - \gamma(\dot{x}(t)) dt \right\}. \quad (2.1)$$

This form supposes that fitness increases additively with net foraging success—a mathematically convenient hypothesis but perhaps less biologically appropriate than one of diminishing returns. The max-operation is performed to avoid non-biological negative values of \mathcal{R}_d that may occur if the foraging strategy expends more energy than it recovers or the environment is of uniformly poor quality. However, since this max will have no effect on our results, and the corners potentially introduced by a max complicate analysis, we will subsequently ignore it, keeping in mind that negative values can either be rounded up to 0, or removed with a vertical shift in $\psi(x)$ and $\gamma(\dot{x})$. For further discussion of the motivation and use of the discounted reproductive number, see Reluga et al. (2009), Thieme (2009), McNamara et al. (2001).

The best migration path $x(t)$ is the one that maximizes \mathcal{R}_d . Using standard methods and results from optimal control theory (Reluga and Shaw 2014), we can derive a Hamiltonian and deduce from Pontryagin's maximum principle that the optimal path can be found by identifying a velocity $u^*(t)$ such that

$$u^* = \operatorname{argmax}_u \psi(x) - \gamma(u) + \lambda u, \quad (2.2a)$$

$$\frac{dx}{dt} = u^*, \quad (2.2b)$$

$$-\frac{d\lambda}{dt} = \frac{\partial \psi}{\partial x}, \quad (2.2c)$$

with the breeding constraint implying the boundary conditions $x(0) = x(T) = 0$. Here, $\lambda(t)$ is an adjoint variable

representing the instantaneous value of movement per unit of velocity u .

Our model is completed by specifying the energy expenditures $\gamma(u)$ and the resource distribution $\psi(x)$. Although there are more complex and accurate models of energy expenditure through movement (Hein et al. 2012), we will adopt a simplified version capturing some basic features and allowing us to obtain exact solutions. Suppose the instantaneous energy use of migration is proportional to the speed of movement but with a hard upper bound on maximum speed, so

$$\gamma(u) = \begin{cases} \frac{|u|}{f} & \text{if } |u| \leq u_{\max}, \\ \infty & \text{otherwise.} \end{cases} \quad (2.3)$$

where f is the movement efficiency parameter and u_{\max} is the maximum speed.

The structure of this system can be represented in terms of two dimensionless groups

$$\hat{\psi} := \frac{\psi f}{u_{\max}}, \quad \hat{\delta} := T\delta,$$

while taking our system variables

$$\hat{t} := \frac{t}{T}, \quad \hat{x} := \frac{x}{Tu_{\max}}, \quad \hat{u} := \frac{u}{u_{\max}},$$

so without loss of generality, we assume the remaining three parameters are normalized to $T = 1$, $f = 1$, $u_{\max} = 1$. The dimensional analysis shows that the time-scale is most naturally measured in terms of the time between breeding events (T), spatial scales are naturally measured in terms of the maximum distance that can be traversed between breeding events (Tu_{\max}), and an increase in the scale the resource availability (ψ) is equivalent to a proportional increase in the efficiency of movement (f).

Applying System (2.2) with Eq. 2.3, any locally optimal movement path must satisfy the first-order conditions

$$\dot{x} = u^*(\lambda), \quad x(0) = x(1) = 0, \quad \dot{\lambda} = -\psi'(x) \quad (2.4a)$$

$$\text{with } u^*(\lambda) = \begin{cases} 1 & \text{if } \lambda > 1, \\ [0, 1] & \text{if } \lambda = 1, \\ 0 & \text{if } -1 < \lambda < 1, \\ [-1, 0] & \text{if } \lambda = -1, \\ -1 & \text{if } \lambda < -1. \end{cases} \quad (2.4b)$$

General analysis

We can say several useful things about optimal strategies before we specify a particular resource distribution $\psi(x)$. System (2.4) specifies an autonomous, two-dimensional boundary-value problem that can be analyzed in a phase

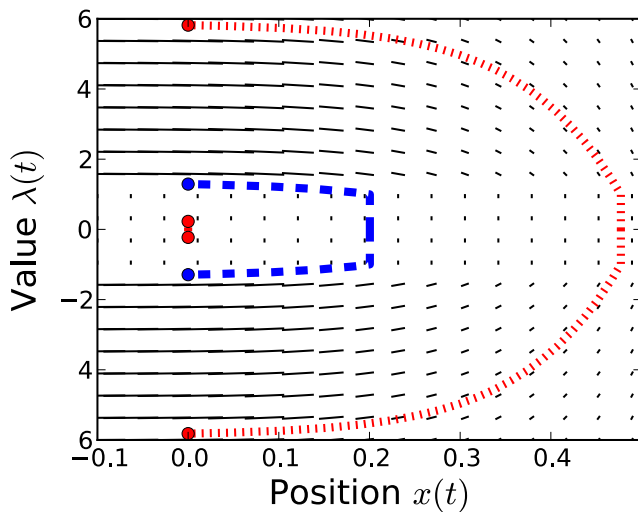


Fig. 1 Direction field for the orbits of System (2.4). The velocity \dot{x} shows jumps when the value of movement $\lambda = \pm 1$, while the rate of change in the value of movement $\dot{\lambda}$ varies smoothly as the displacement x gets larger. Optimal paths correspond to orbits with the boundary conditions $x(0) = x(1) = 0$. In this case, there are three such orbits, two local maxima (red dotted), and one additional critical orbit (blue dashed). Parameter values: $A = 50$, $s = 0.7$, $k = 10$, $A_{\min} = 0$. This corresponds to the $k = 10$ case in Fig. 3

plane. From Fig. 1 and supporting analysis, we discover that for any constant monotone resource distribution $\psi(x)$ the optimal path connecting $x(0) = 0$ to $x(1) = 0$ must have the very simple piecewise form

$$x(t) = \min \left(z, \frac{1}{2} - \left| t - \frac{1}{2} \right| \right), \quad (3.1)$$

where z is the optimal maximum migration distance traveled by an individual and satisfies the inequalities $0 \leq z \leq 1/2$. For simplicity, from here onward, we refer to the optimal movement path $x(t)$ in terms of the corresponding optimal maximum distance z . The exact value of z must determined

based on System Eq. 2.4, such that either $\lambda(z) = 1$ and $\lambda(1 - z) = -1$ or $x(t) = 0$ and $|\lambda(t)| \leq 1$. But candidate z values are more intuitively identified as maxima of \mathcal{R}_d . The fitness under Eqs. 2.3 and 3.1 as a function of z is

$$\mathcal{R}_d(z) = e^{-\delta} \left\{ 2 \int_0^z \psi(v) dv + (1 - 2z)\psi(z) - 2z \right\}. \quad (3.2)$$

The local sensitivity of the discounted reproductive number \mathcal{R}_d to the maximum migration distance

$$\frac{d\mathcal{R}_d}{dz} = e^{-\delta} [(1 - 2z)\psi'(z) - 2] \quad (3.3)$$

shows us how trade-offs in the choice of maximum distance play out. The marginal costs of movement per unit change in the maximum distance are constant (-2). If the resource distribution is increasing ($\psi'(z) > 0$), migrating a little farther will give better feeding, but the extra travel distance will reduce the amount of time that can be spent there. In the case of maximal migration ($z = 1/2$), the individual must turn around and begin migrating back to the breeding ground as soon as the maximum distance is reached. This trade-off between the costs and benefits of farther migration means that the best migration distance is always less than $1/2$. Residence (no migration at all, $z = 0$) will be locally optimal when $\psi'(0) < 2$. Reverting to dimensional variables, residence is locally optimal if $fT\psi'(0)/2 < 1$. So, a weaker resource gradient, lower efficiencies, and shorter breeding cycles discourage migration.

More global information can be obtained by determining which resource distribution leads to an evolutionarily neutral model (i.e., when all z strategies have equal fitness). Setting $d\mathcal{R}_d/dz = 0$ in Eq. 3.3, we find that discounted reproductive value is constant in z when

$$\psi'(z) = \frac{2}{1 - 2z}. \quad (3.4)$$

Table 1 Model parameters and units

Symbol	Interpretation	Units
t	Time	Time
$x(t)$	Animal position	Distance
$u(t)$	Animal velocity	Distance per time
u_{\max}	Maximum speed	Distance per time
δ	Discount rate	Per time
T	Breeding cycle duration	Time
$\gamma(\dot{x})$	Movement expenditures	Energy per time
f	Movement efficiency	Distance per energy
$\psi(x)$	Resource distribution	Energy per time
A	Total cline resource variation	Energy per time
A_{\min}	Cline resource minimum	Energy per time
s	Cline resource distribution shift	Distance
k	Cline resource distribution shape	Per distance

This ordinary differential equation has general solutions

$$\psi_{\text{neutral}}(x; C) := C - \ln(1 - 2x) \quad (3.5)$$

for any constant C . These solutions correspond to a family of perfectly neutral static resource distributions—if $\psi(z) = \psi_{\text{neutral}}(z; C)$ for some C , every migration of the form of Eq. 3.1 has the same reproductive value for $z \in [0, 1/2)$. The singularity at $z = 1/2$ is an indicator that optimal migration is always less than half the maximum distance an individual can travel in a breeding cycle, as explained above. One of the implications of $\psi_{\text{neutral}}(x; C)$ is that for any other static smooth resource distribution ψ such that $\psi''(x) < \psi''_{\text{neutral}}(x)$ everywhere (including all concave resource distributions), there will be a unique locally optimal migration strategy that is also globally optimal. On the other hand, wiggly resource distributions with multiple tangent points can have multiple local maxima in the reproductive number (see Fig. 3).

Analysis of a logistic cline

To illustrate how spatial heterogeneity in resource distribution and spatial constraints on reproduction can create bi-modality in fitness, we will use a simple resource cline. Define a resource distribution $\psi(x)$ that is a static logistic function;

$$\psi(x) := \frac{(A + A_{\min}) + e^{k(s-x)} \min}{1 + e^{k(s-x)}} \quad (4.1)$$

with minimum resource availability $\min \geq 0$, cline height parameter $A > 0$, position-shift parameter s , and shape parameter $k > 0$. The geometry of this cline assumption includes local domains that are flat, linear, concave, and convex, so we can explore much of the range of possible shapes that come to mind. The shape parameter k controls the cline's sharpness, with small- k corresponding linear increases in resource, while large- k correspond to Heaviside functions where resource availability jumps abruptly at $x = s$.

This completely specifies our model, with parameters and their units summarized in Table 1. When we nondimensionalize with

$$\hat{A} := \frac{Af}{u_{\max}}, \quad \hat{A}_{\min} := \frac{A_{\min}f}{u_{\max}}, \quad \hat{s} := \frac{s}{Tu_{\max}}, \quad \hat{k} := kTu_{\max}$$

and subsequently discard the hat-notation, we find

$$\dot{\lambda} = \frac{-Ake^{k(s-x)}}{(e^{k(s-x)} + 1)^2}. \quad (4.2)$$

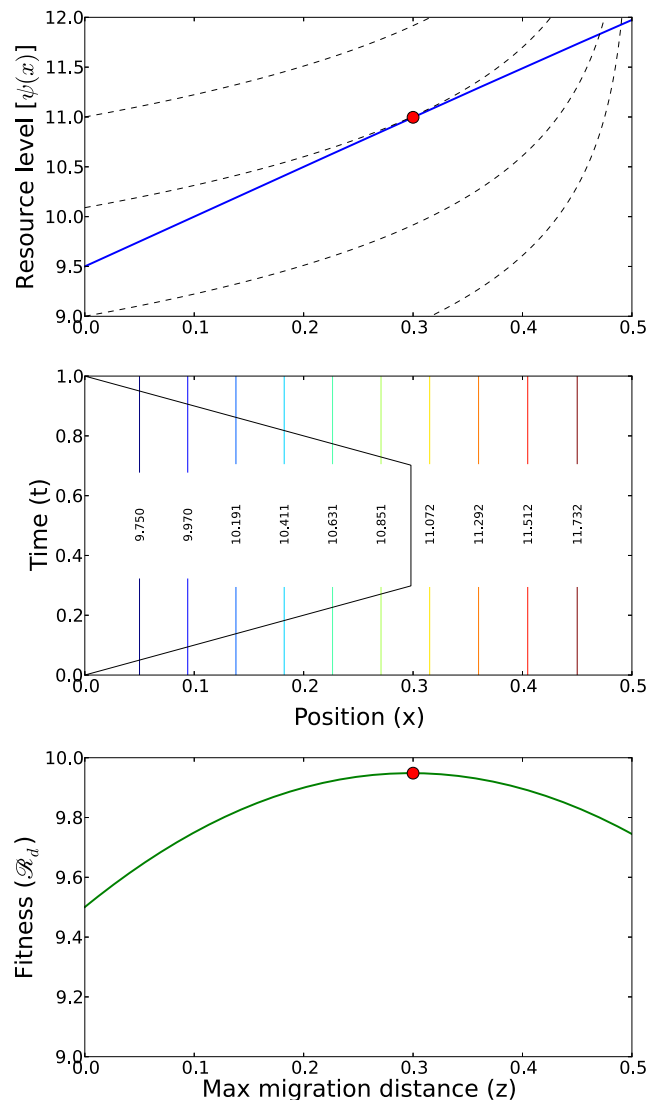


Fig. 2 Plots of a near-linear resource distribution $\psi(x)$ (top, solid blue) accompanied by several neutral resource distribution contours $\psi_{\text{neutral}}(x)$ (top, dashed), one period of the corresponding optimal migration strategy (middle, solid black) along with resource contours (middle, colored), and the reproductive values of candidate migration strategies from Eq. 3.1 as a function of maximum migration distance z as given by Eq. 2.1 (bottom). The resource gradient's linear slope (about 5) is large enough to offset the costs of movement. The most fit strategy (bottom, red dot) is also a point where the resource distribution curve is tangent to a neutral resource contour (top, red dot). Parameter values $A = 20$, $k = 1$, $s = 0.1$

The fitness under Eq. 4.1 as a function of z is

$$\mathcal{R}_d(z) = e^{-\delta} \left\{ 2z(A - 1) + \frac{A(1 - 2z)}{e^{k(s-z)} + 1} + \frac{2A}{k} \log \left(\frac{e^{k(s-z)} + 1}{e^{ks} + 1} \right) + A_{\min} \right\}. \quad (4.3)$$

By differentiating Eq. 4.4 with respect to z and using any common one-dimensional root-finding method such as

Mueller's method, locally and globally optimal migration strategies can be efficiently and accurately determined for any parameter values. An example is shown in Fig. 2. In general, there may be more than 1 local maximum in the reproductive number (see Fig. 3). Note that while resource minimum A_{\min} appears in \mathcal{R}_d , the difference in reproductive value between strategies is independent of A_{\min} .

When the shape parameter k is small such that the curvature is small, the resource gradient over $[0, 1/2]$ can be approximated by a line. Let z^* represent the migration distance that maximizes the reproductive value. Under a linear approximation $\psi(x) \approx \psi(0) + \psi'(0)x$, the reproductive value

$$\mathcal{R}_d(z) \approx e^{-\delta} \left\{ \psi(0) + (\psi'(0) - 2)z - \psi'(0)z^2 \right\} \quad (4.4)$$

and the optimal migration distance is then

$$z^* = \max \left\{ 0, \frac{1}{2} - \frac{1}{\psi'(0)} \right\}. \quad (4.5)$$

The steeper the resource gradient, the farther an individual should move.

We can further analyze Eq. 4.4 to characterize the properties of the optima under different conditions. By differentiating the reproductive value to identify local maxima, we find z^* must solve the transcendental equation

$$Ak(1 - 2z^*) = 4\cosh(kz^* - ks) + 4. \quad (4.6)$$

At the movement extremes, $z = 1/2$ is never a local maximum but $z = 0$ is a local maximum if

$$A < \frac{4 + 4\cosh(ks)}{k}, \quad (4.7)$$

corresponding to our requirement that $\psi'(0) < 2$ for linear gradients. Heuristically, the resource cline promotes migration if its midpoint is close enough to the breeding ground and the gradient is steep enough.

Since hyperbolic cosine is convex, no more than two interior local extreme solving Eq. 4.6 can ever coexist. Using calculus techniques, we can determine that two local maxima can only coexist when

$$A > \frac{8k}{k^2 - 4}. \quad (4.8)$$

The bifurcation structure of the extremes of the reproductive value is summarized in Fig. 4. If the resource cline height (A) is small, then the optimal strategy is not to move. If the resource cline height is large (A is large) and the transition is sharp (k is large), then as we vary the cline position s , there will be a transitional regime between migration and residency where two different local maxima will appear for values of the cline midpoint that are farther from the breeding site (see Fig. 4). In between, there is a region where there is always a unique globally optimal movement strategy (see Fig. 4).

Density dependence

There are many different ways density-dependent limits on population growth can enter into migration theory, and the specifics of how they enter can have important implications for the coexistence of migration strategies. For example, if migrant and resident populations are regulated independently by density-dependent mortality that occurs between breeding events (i.e., “soft” selection, (Christiansen 1975; Débarre and Gandon 2011)), the coinvasion of migrant and resident types for steep clines is preserved. On the other hand, if density dependence acts uniformly across the population (“hard” selection) or is exerted at the time of reproduction, migrants and residents may be directly competing, and only the most fit subpopulation will persist. In this particular case, individuals might increase their fitness by returning to breed less often. Allowing this would not alter our results. Overall, these results support previous findings (Kaitala et al. 1993) that partial non-breeding migrations can occur without environmental stochasticity, as long as density-dependent regulation of migrants and non-migrants occurs during the non-breeding season.

As an example of migration theory where populations are primarily constrained by spatially distributed resource depletion, we make use of the concept of grazing pressure. Let allocation $I(z)$ be a measure of the number of animals in the population using each migration strategy z . For every strategy z , $I(z) \geq 0$. When animals using strategy z follow the path $x(t, z)$ over the course of the year and consume at a constant rate over time, the total annual grazing pressure at each location u will be given by the formula

$$p(u) := \int_0^{1/2} \int_0^1 I(z) \delta(u - x(t, z)) dt dz \quad (5.1)$$

where $\delta()$ is Dirac's delta-function (not to be confused with our discounting parameter δ). Assuming individuals follow migration paths of the form of Eq. 3.1, the annual grazing pressure can be simplified to

$$p(x) = (1 - 2x)I(x) + 2 \int_x^{1/2} I(z) dz. \quad (5.2)$$

To get further, we propose that the annual dynamics of the resource distribution $\psi_t(x)$ are governed by the linear difference equation

$$\psi_{t+1}(x) = \max\{0, \beta\psi_t(x) + r(x) - p(x)\} \quad (5.3)$$

where β is the fraction of resource persisting from the previous season, $r(x)$ is the annual resource inflow at all locations x , and $p(x)$ is the annual grazing pressure con-

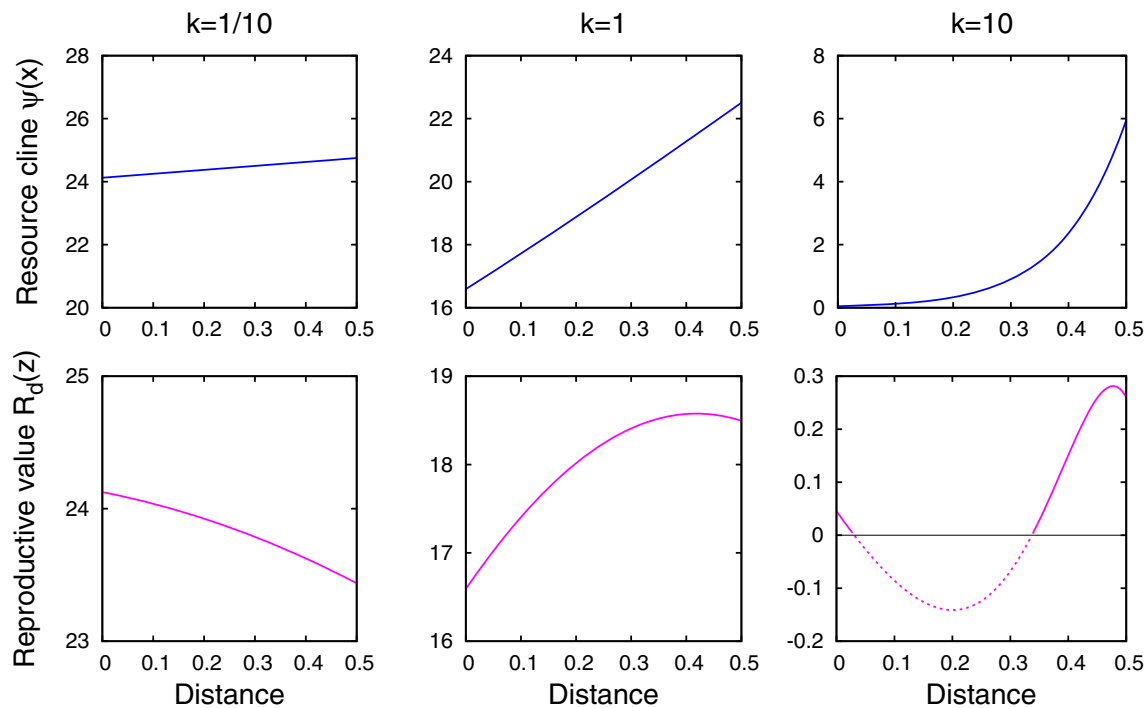


Fig. 3 These plots show the nonlinear dependence of the discounted reproductive value $\mathcal{R}_d(z)$ on the maximum migration distance z for three cline shapes. When the resource cline is shallow (left, $k = 1/10$), reproductive value declines monotonely with migration distance. For a moderate linear cline (middle, $k = 1$), an intermediate migration

distance dominates. For a steeply accelerating cline (right, $k = 10$), there can be two local optima; $z = 0$ has become a local maximum because the benefits of movement only come to fruition if a relatively flat region of the resource cline is fully crossed to reach a regions of higher resource concentration. Parameters: $A = 50$, $A_{\min} = 0$, $s = 0.7$

suming resource. Over time, the resource distribution will converge to the steady-state

$$\bar{\psi}(x) := \max \left\{ 0, \frac{r(x) - p(x)}{1 - \beta} \right\}. \quad (5.4)$$

Under an equilibrium resource distribution $\bar{\psi}$, the fitness $\mathcal{R}_d(z)$ of a strategy z can be determined by Eq. 3.2. So, from an allocation, we can determine the grazing pressure over space. From the grazing pressure, we can determine the equilibrium resource distribution. And from the equilibrium resource distribution, we can determine the fitness of each strategy. Thus, the fitness in the presence of resource depletion can be thought of as a function of the strategy allocation $(\mathcal{R}_d(z; I))$.

Under the pessimism principle (Mylius and Diekmann 1995), a stable allocation I^* is one for which no alternative strategy can invade successfully ($\max_z \mathcal{R}_d(z; I^*) = 1$) and no unsustainable strategy is used (for every strategy z where $I^*(z) > 0$, $\mathcal{R}_d(z; I^*) \geq 1$). These conditions provide a set of equations from which we can attempt to identify a stable allocation I^* (see Appendix A). It appears to be an open mathematical question as to when a stable allocation can be found, and if there are more than one for a given system. However, using numerical fixed-point methods, we can calculate some examples of stable allocations for

different resource influx functions (see Figs. 5, 6, 7, and 8). Interestingly, in these special cases, it appears that the stable allocation I^* will be stable not just against invasion by movement strategies of the form of Eq. 3.1, but against all possible movement strategies; the steady-state resource distribution $\bar{\psi}(x)$ is capped at levels that are too low to offset any movement costs. This would differ from results on ideal-free distributions in reaction–diffusion systems where alternatives to random-movement strategies might still be invaded (Lam and Munther 2014).

Discussion

Here, we have used optimal control methods to exactly solve for the best movement path, given specific costs from movement and payoff from different resource distributions. Dimensional analysis reveals that the importance spatial variation in resource distributions depends on the speed and efficiency with which animals can access the resources. We have then shown that changing the shape of the resource distribution alone shifts whether purely migration, purely residency, or both are favored as the optimal movement pattern. The coinvasion of movement strategies can be interpreted in two ways.

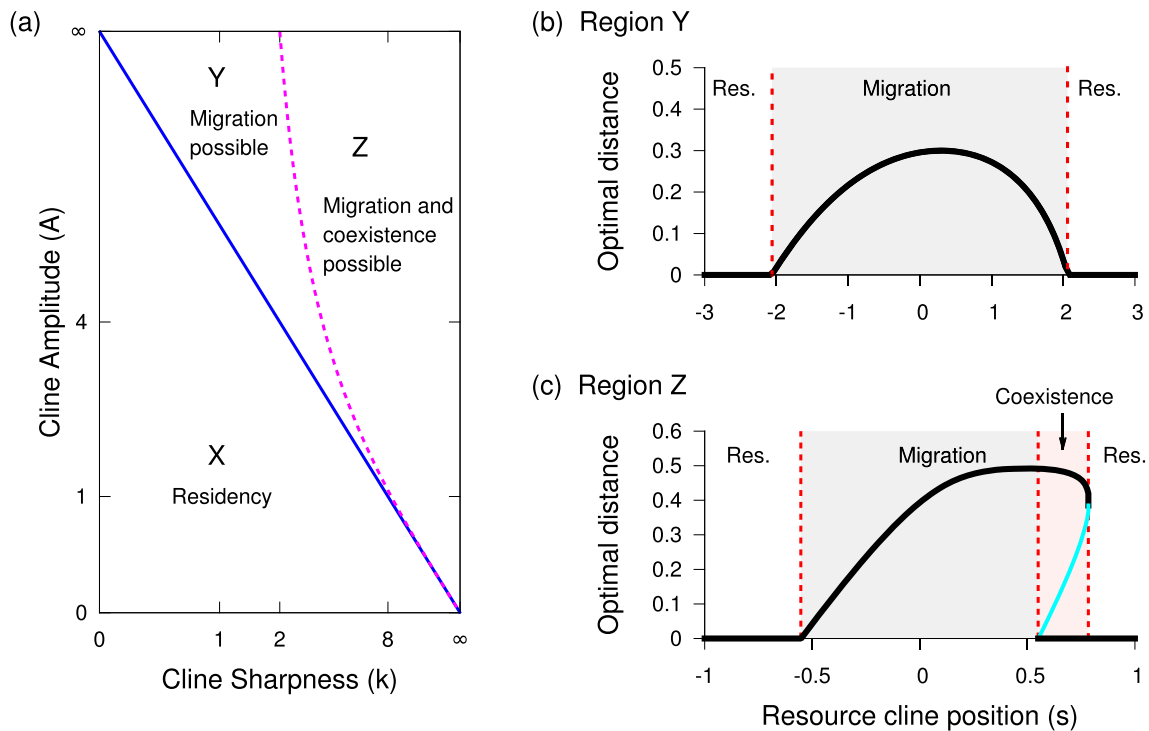


Fig. 4 **a** The $A \times k$ parameter space (in hyperbolic coordinates) can be dissected into three regions. In region X, the cost of movement always outweighs the potential resource gains, and the best strategy is reside in the breeding-ground year-round ($x(t) = 0$ for all t). In region Y, the optimal strategy depends on the position of the resource cline, but there is always just 1 locally and globally optimal strategy (**b**); when the cline's midpoint is close to the breeding ground ($s \approx 0$), the best

strategy will be migration, but when the cline's midpoint is far from the breeding ground ($|s| \gg 0$), movement costs out-weigh resource gains. In region Z, the best movement strategy still depends on the cline's position s (see **c**), but there may be two local resource maxima. In the case of (**c**), for shift values $s \in (0.55, 0.79)$, there are two local maxima. Parameter values: **b** $A = 20$, $k = 1$; **c** $A = 50$, $k = 10$

First, coinvasion of migrant and resident types can be interpreted as partial migration, where both types occur simultaneously within the same population. Our model corresponds to the case of partial non-breeding migration where migrants and residents share a breeding site. Unlike all previous models of partial migration, our model

is spatially explicit and directly accounts for the types of ecological conditions that select on movement strategies.

Second, coinvasion of migrant and resident types can be interpreted as coinvasion of two species with different movement strategies on a single resource. In this case, it is possible that a branching of movement strategies was a

Fig. 5 A stable strategy allocation $I^*(z)$ when resource accumulates according to a linear gradient $r(x) = 2 - 4x$. Also show are the corresponding equilibrium resource distribution, $\bar{\psi}$, and the reproductive values of each strategy, $R_d(z; I)$. Non-migratory strategies are the most frequently used. Parameters $\beta = 0.4$, $\delta = 0.1$

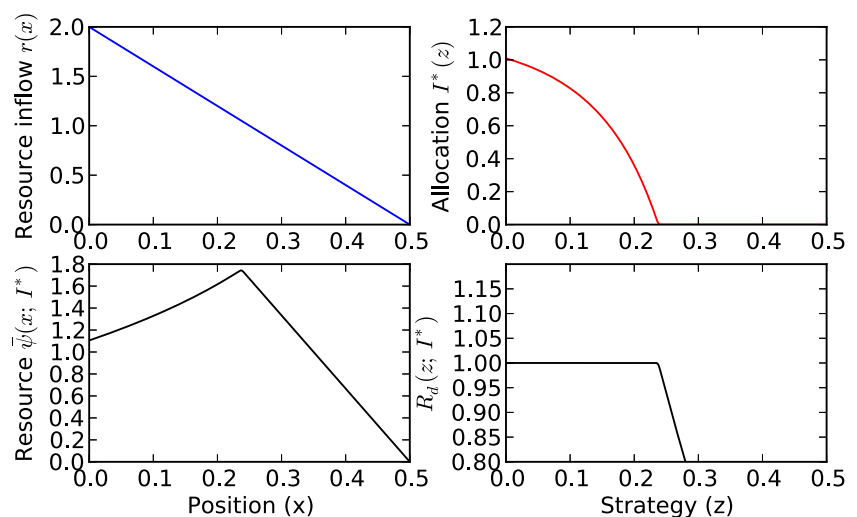


Fig. 6 Same as Fig. 5 but with resource accumulating under a logistic cline $r(x) = 1 + (1 + \exp(-50(x - 0.35)))^{-1}$. The allocation solution is bimodal, containing both resident and migratory strategies. Parameters $\beta = 0.4$, $\delta = 0.1$

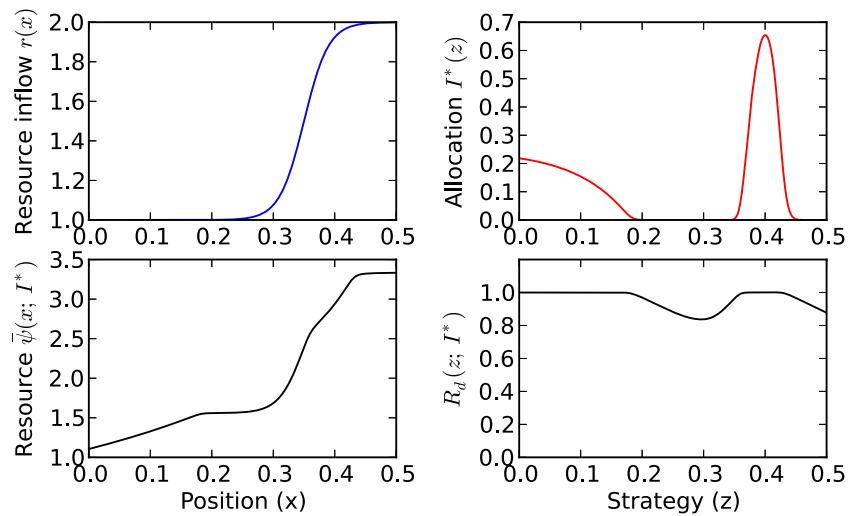


Fig. 7 A stable strategy allocation $I^*(z)$ solving System (A.1) when resource accumulates according to an increasing linear gradient $r(x) = 9x$. Also show are the corresponding equilibrium resource distribution, $\bar{\psi}$, and the reproductive values of each strategy, $\mathcal{R}_d(z; I)$. The allocation is dominated by long migrations. Parameters $\beta = 0.4$, $\delta = 0.1$

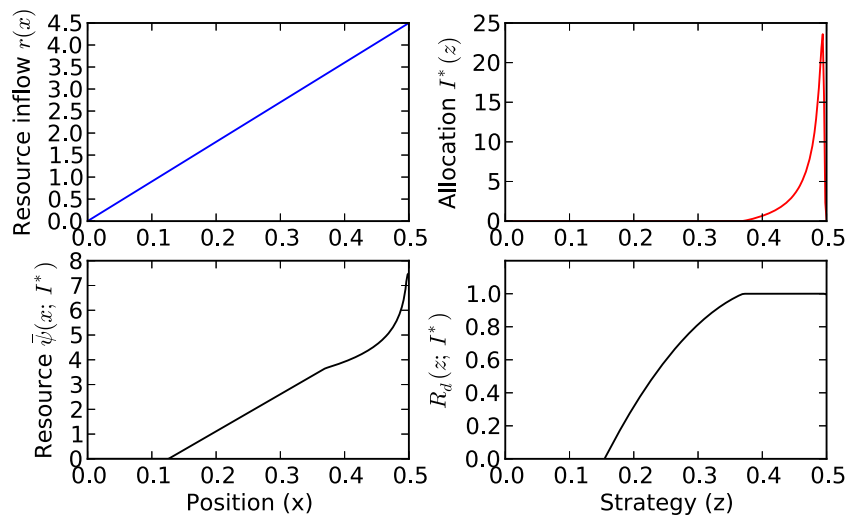
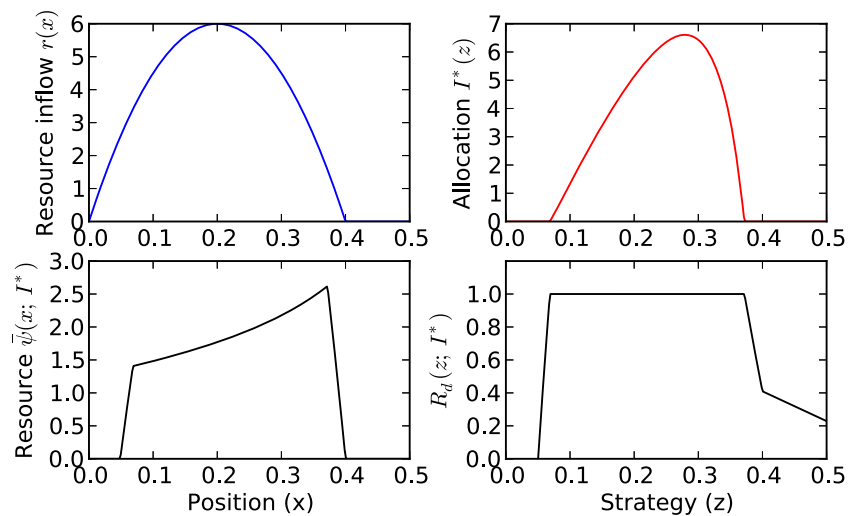


Fig. 8 Same as Fig. 7 but with resource accumulating around a single peak according to $r(x) = 60x - 150x^2$. Only strategies that migrate an intermediate distance are allocated. Parameters $\beta = 0.4$, $\delta = 0.1$



precursor to the speciation event, a process that has been suggested in the case of coexistence of dispersal types (Doebeli and Ruxton 1997; Mathias et al. 2001; Bode et al. 2011).

While our results provide some insight, a number of open problems remain, particularly with respect to the evolution of movement when populations themselves alter their environments. A simple special case is proposed in “Density dependence”, but even basic mathematical results for it remain unknown. While we generally expect the results to be consistent with those already obtained regarding the evolution of dispersal (Holt and Barfield 2001), computational experiments and mathematical analysis of spatially-explicit scenarios could deepen our theoretical understanding of the importance of specific ecological conditions. Computational experiments could also help us to understand the relationship between the optimal strategies we have identified and the time-dependent and path-dependent aspects of evolution and speciation that can lead up to these optima. It could also be useful to expand on our approaches so that they may approximate the current situations of extant species and anticipate situations where adaptive responses to climate change will be more difficult.

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Appendix A: On ideal migration allocations

Based on the description in “Density dependence”, a stable allocation $I^*(z)$ over strategies z must solve the nonlinear integral system

$$\forall z \in [0, 1/2], \quad I^*(z) [1 - \mathcal{R}_d(z; I^*)] = 0, \quad (\text{A.1})$$

$$\mathcal{R}_d(z; I^*) = e^{-\delta} \left\{ 2 \int_0^z \bar{\psi}(v; I^*) dv + (1-2z) \bar{\psi}(z; I^*) - 2z \right\}, \quad (\text{A.2})$$

$$\bar{\psi}(x; I^*) = \max \left\{ 0, \frac{r(x) - p(x; I^*)}{1 - \beta} \right\}, \quad (\text{A.3})$$

$$p(x; I^*) = (1 - 2x)I^*(x) + 2 \int_x^{1/2} I^*(z) dz. \quad (\text{A.4})$$

for given parameters δ , β , and resource inflow $r(x)$. Extra example solutions are shown in Figs. 7 and 8.

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