

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

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## ABSTRACT

20 Organismal movement can take on a variety of spatial and temporal  
forms. These forms depend in part on the type and scale of environment  
22 experienced as well as the internal state of the individual. However, indi-  
viduals experiencing seemingly the same environment on the same time  
24 scale can display different movement strategies. Here we consider the  
case where movement is costly and individuals must return to a common  
26 breeding ground annually to reproduce. We derive the optimal movement  
strategy, given specific movement costs and environmental resource dis-  
tributions. We find, intuitively, that large resource clines favor migratory  
28 behavior, and small resource clines favor residential behavior. However  
we also show that when resource clines are sharp, migrants and residents  
30 can coexist with each exploiting a locally optimal behavior. This can be  
interpreted as an example of partial migration (if migrants and residents  
32 are members of the same species). Alternatively, this can also be inter-  
preted as two recently divergent species coexisting on a single resource,  
34 using different movement strategies to share the niche. We conclude with  
a discussion of density-dependent pressures on movement, including local  
36 resource depletion.

## 1. Introduction

38

Movement is ubiquitous among living organisms (particularly animals) and is  
 40 vital for the long-term persistence and survival of any population (Hanski 1999). A  
 large diversity of movement patterns are found in nature, spanning a range of  
 42 temporal and spatial scales. These can vary from e.g. foraging movements of  
 nematodes *Caenorhabditis elegans* on the scale of minutes and centimeters  
 44 (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  
 46 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  
 48 external and internal (Cresswell et al. 2011; Clobert et al. 2012). Intuitively,  
 different movement types can be favored by different environments, the same  
 50 environment experienced on different scales, or by individuals with different  
 abilities or internal states. However, particularly intriguing are cases where the  
 52 same environment experienced by similar individuals on similar scales appears to  
 select for different movement strategies.

54 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  
 56 not (Lundberg 1988). Partial migrations can be clustered among three distinct  
 types (Shaw and Levin 2011): non-breeding partial migration where migrants and  
 58 non-migrants breed together but spend the non-breeding (e.g. winter) season apart;  
 breeding partial migration where migrants and non-migrants spend the  
 60 non-breeding season together and breed apart; and skipped-breeding partial  
 migration where individuals must migrate to breed and non migrants do not breed  
 62 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  
 64 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

66 their level of energy stores (e.g. [Thorpe 1994](#); [Caut et al. 2008](#)) thus the  
coexistence of different movement types can be accounted for by individuals  
68 differing in internal state.

However, the cause of coexistence between migrant and non-migrant  
70 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  
72 survival during the non-breeding period to explain the coexistence of migrant and  
non-migrant types ([Cohen 1967](#); [Lundberg 1987](#)). [Kaitala et al. \(1993\)](#)  
74 demonstrated theoretically that non-breeding partial migrations could be  
maintained by separate density-dependent regulation of migrant and non migrant  
76 types during the non-breeding season, without invoking environmental uncertainty.  
More recent models have focused on combinations of density-dependent,  
78 density-independent, and stochastic factors in maintaining partial migration  
([Griswold et al. 2010](#); [Vélez-Espino et al. 2013](#)). In the case of breeding partial  
80 migrations, [Taylor and Norris \(2007\)](#) determined that density-dependence during  
the non-shared season is necessary for the coexistence of migrant and non-migrant  
82 types.

All of these models of partial migration include space only implicitly. Since  
84 migration is fundamentally an adaptive response to spatially distributed resources  
([Cresswell et al. 2011](#)), spatially explicit models may provide insights that spatially  
86 implicit ones cannot. Furthermore, existing partial migration models also only  
indirectly consider ecological conditions as experienced through survival. Migration  
88 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)  
90 ecological conditions ([Alerstam et al. 2003](#)). Therefore by explicitly considering the  
ecological conditions that individuals face (rather than indirect effects through  
92 survival) we may gain a deeper understanding of the conditions favoring migrant  
and non-migrant strategies and potentially how changes in conditions may favor

94 switches in strategies adopted by individuals.

In a recent paper (Reluga and Shaw 2014), we described how the tendency of  
96 some species to migrate could be understood in a spatially explicit setting as fitness  
optimization balancing movement costs with foraging success on a single resource.  
98 However, that analysis was limited mostly to numerical results. In this paper, we  
present exact closed-form solutions for optimal migration on a stationary resource  
100 cline when reproduction is constrained to occur annually on an isolated breeding  
ground. We find that some ecological conditions favor migration, others favor  
102 residency, and a subset of conditions support coexistence between resident and  
migratory strategies. This scenario illustrates how seasonal constraints on life  
104 history and in combination with costly movement can bifurcate the niche space,  
allowing for the potential co-existence of resident and migratory subpopulations  
106 (partial migration) or the coexistence of two species with different movement types,  
on a single resource. We conclude with a consideration of density-dependent effects.  
108 These results provide further evidence that partial migrations can evolve under  
local density dependence even without environmental variation.

110

## 2. Model

In an idealized evolutionary model of migration, we look at the case where an  
112 individual’s reproductive success is determined by her foraging success over a  
lifetime, minus energy expenditures. Consider a semelparous species in a  
114 1-dimensional habitat with a shared breeding ground at location  $x = 0$ . Adults are  
obligated to return to the breeding ground every year (or more generally, every  $T$   
116 time units) to reproduce. Between breeding events, an individual may die with  
mortality risk  $\delta$  per unit time, independent of location, behavior, state, or time of  
118 year. The reproductive success of surviving individuals depends on foraging success  
minus expenditures. When forage abundance is described by a resource distribution  
120  $\Theta(x, t)$  in space and time, and energy expenditure depends only on the speed of

movement, given 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

$$\mathcal{R}_d := e^{-\delta T} \int_0^T [\Theta(x(t), t) - \gamma(\dot{x}(t))] dt. \quad (2.1)$$

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 optimal 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 deduce that the optimal path can be found by identifying a velocity  $u^*(t)$  such that

$$u^* = \max_u \lambda u - \gamma(u), \quad (2.2a)$$

$$\dot{x} = u^*, \quad (2.2b)$$

$$-\dot{\lambda} = \frac{\partial \Theta}{\partial x}, \quad (2.2c)$$

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.

Our model is completed by specifying the energy expenditures  $\gamma(u)$  and the resource distribution  $\Theta(x, t)$ . 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.

To illustrate how spatial heterogeneity in resource distribution and spatial constraints on reproduction can create bi-modality in fitness, we will use a simple

140 resource cline. Define a resource distribution that is a static logistic function;

$$\Theta(x, t) := \psi(x) = \frac{(A + A_{\min}) + e^{k(s-x)} A_{\min}}{1 + e^{k(s-x)}} \quad (2.4)$$

with height parameters  $A > 0$ , position-shift parameter  $s$ , and shape parameter  
 142  $k > 0$ . The geometry of this cline assumption includes local domains that are flat,  
 linear, concave, and convex, so we can explore most of the range of possible shapes  
 144 that come to mind.

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

### 3. Analysis

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

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

while taking our system variables

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

148 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 the  
 150 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  
 152 can be traversed between breeding events ( $Tu_{\max}$ ), and increasing the amplitude of  
 the gradient ( $A$ ) is equivalent to a proportional increase in the efficiency of  
 154 movement ( $f$ ).

Applying System (2.2) with Eqs. (2.3) and (2.4), any locally optimal

Table 1: Model parameters and units.

Symbol	Interpretation	Units
$t$	time	time
$x(t)$	animal position	distance
$u(t)$	animal velocity	distance per time
$\delta$	discount rate	per time
$T$	annual cycle length	time
$\gamma(\dot{x})$	movement expenditures	energy per time
$f$	movement efficiency	distance per energy
$u_{\max}$	maximum speed	distance per time
$\psi(x)$	resource distribution	energy per time
$A$	total resource variation	energy per time
$A_{\min}$	resource minimum	energy per time
$s$	resource distribution shift	distance
$k$	resource distribution shape	per distance



156 movement path must satisfy the first-order conditions

$$\dot{x} = u^*(\lambda), \quad x(0) = x(1) = 0, \quad \dot{\lambda} = -\psi'(x) = \frac{-Ak e^{k(s-x)}}{(e^{k(s-x)} + 1)^2}, \quad (3.1a)$$

$$\text{with } u^*(\lambda) = \begin{cases} 1 & \text{if } \lambda > 1, \\ [0, 1] & \text{if } \lambda = 1, \\ 0 & \text{if } -1 < \lambda < 1, \\ [-1, 0] & \text{if } \lambda = -1, \\ -1 & \text{if } \lambda < -1. \end{cases} \quad (3.1b)$$

System (3.1) specifies an autonomous, two-dimensional boundary-value  
 158 problem that can be analyzed in a phase-plane. From Figure 1, we discover that  
 the optimal path must have the very simple piecewise form

$$x(t) = \min \left( z, \frac{1}{2} - \left| t - \frac{1}{2} \right| \right), \quad (3.2)$$

160 where  $z$ , the maximum migration distance traveled by an individual, is some real  
 number satisfying  $0 \leq z \leq 1/2$ . The reproductive value under Eq. (2.4) as a  
 162 function of  $z$  is

$$\mathcal{R}_d(z) = e^{-\delta} \left\{ (1 - 2z)\psi(z) - 2z + 2 \int_0^z \psi(t) dt \right\} \quad (3.3)$$

$$= e^{-\delta} \left\{ 2z(A - 1) + \frac{A(1 - 2z)}{e^{k(s-z)} + 1} + \frac{2A}{k} \log \left( \frac{e^{k(s-z)} + 1}{e^{ks} + 1} \right) + A_{\min} \right\}. \quad (3.4)$$

From Eq. (3.4), locally and globally optimal migration strategies can be determined  
 164 exactly for all parameter values. An example is shown in Figure 2. In general,  
 there may be more than 1 local maximum in the reproductive number (see  
 166 Figure 3). Note that while resource minimum  $A_{\min}$  appears in  $\mathcal{R}_d$ , it does not  
 change the locations of any resource maxima.

168 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  
 170 migration distance that maximizes the reproductive value. Under a linear

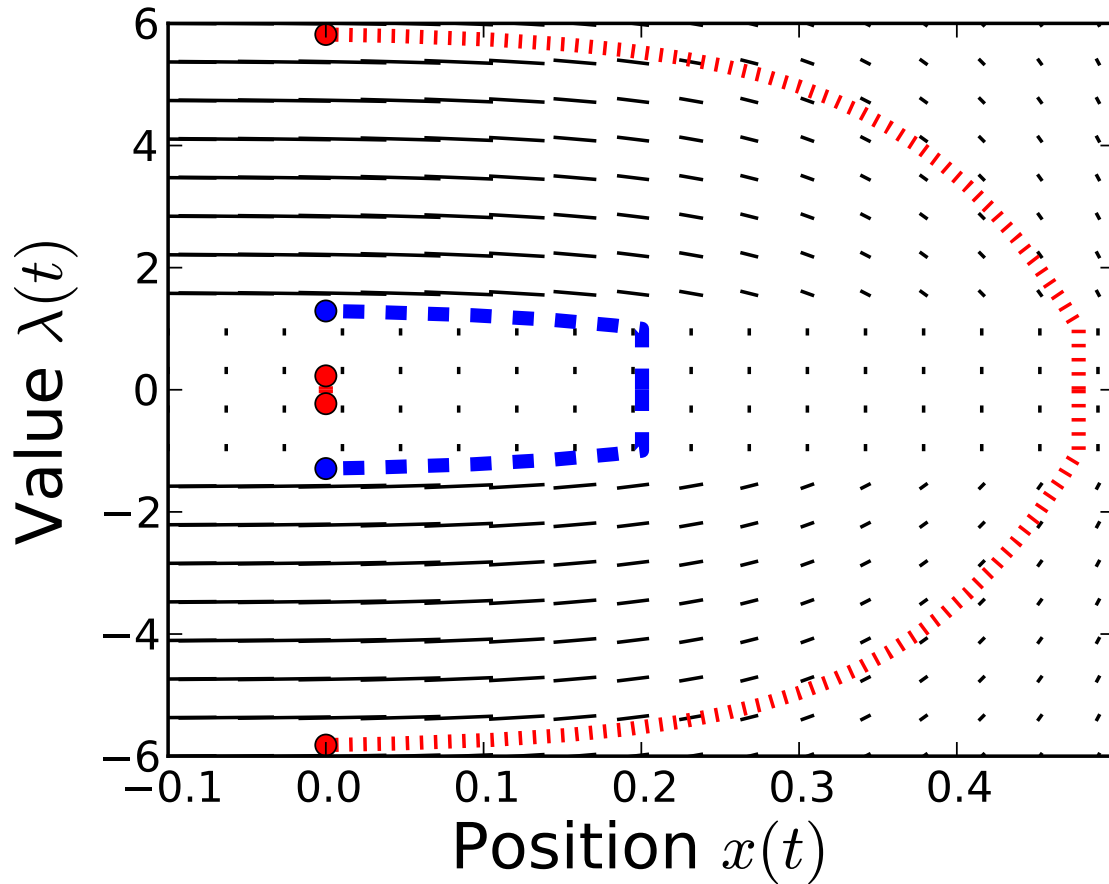


Fig. 1.— Direction field for the orbits of System (3.1). The velocity  $\dot{x}$  shows jumps when the movement-value  $\lambda = \pm 1$ , while the rate of change in the movement-value  $\dot{\lambda}$  varies smoothly as the displacement  $x$  gets larger. Optimal paths correspond to orbits with the boundary conditions  $x(0) = x(1) = 0$ . In this case, there are three such orbits, two local maxima (red dotted) and one saddle point (blue dashed). Parameter values:  $A = 50$ ,  $s = 0.7$ ,  $k = 10$ .

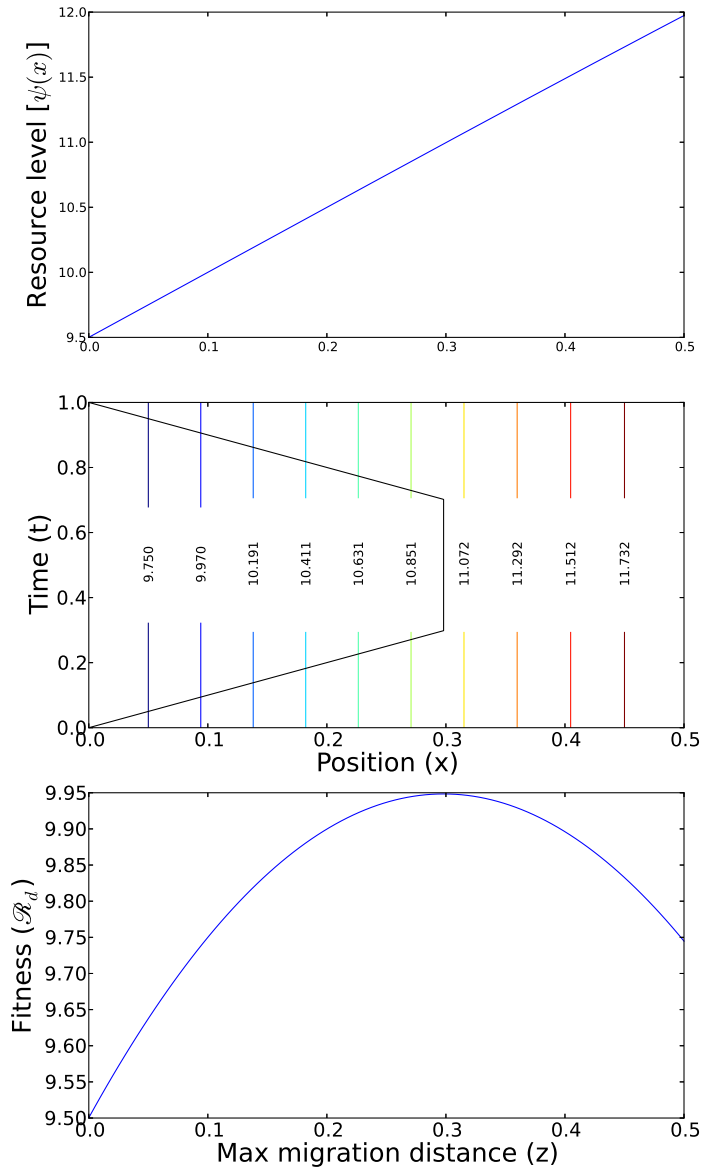


Fig. 2.— Plot of a near-linear resource distribution (top), one period of the corresponding optimal migration strategy (middle), and the fitness of candidate migration strategies (Eq. (3.2)) as a function of maximum migration distance  $z$  as given by Eq. (2.1) (bottom). The resource gradient (about 5) is large enough to offset the costs of movement. Parameter values  $A = 20$ ,  $k = 1$ ,  $s = 0.1$ .

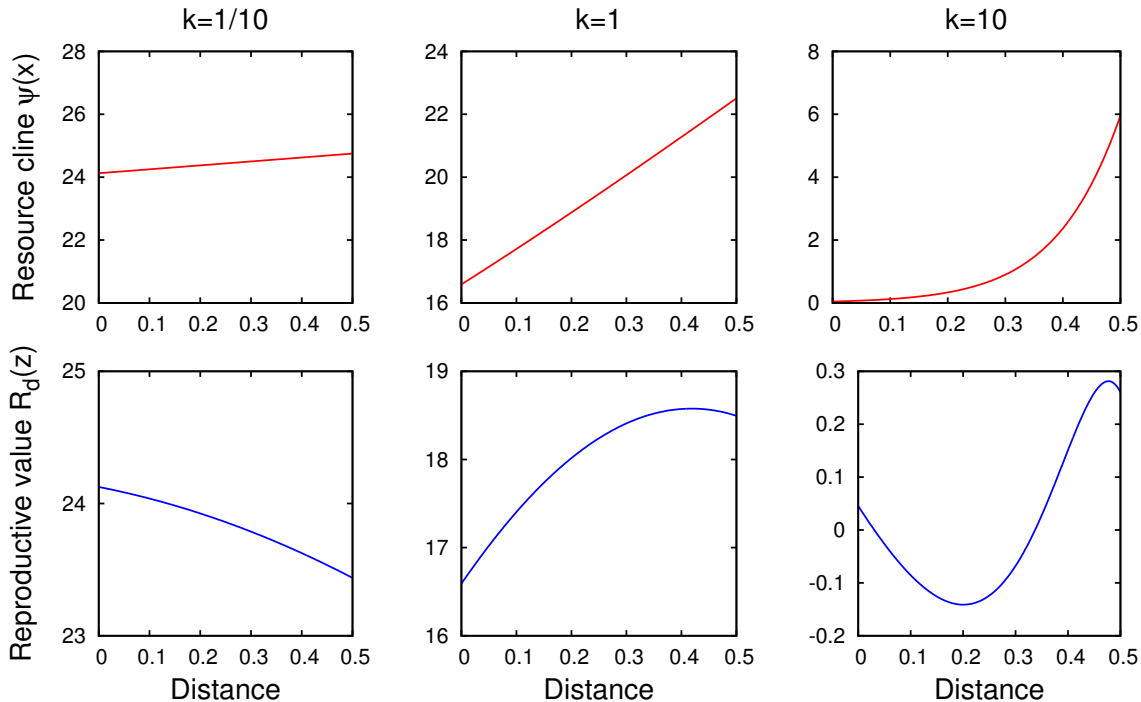


Fig. 3.— These plots show the nonlinear dependence of the discounted reproductive value  $\mathcal{R}_d(z)$  on the maximum migration distance  $z$  for three cline shapes. When the resource cline is shallow (left,  $k = 1/10$ ), reproductive value declines monotonely with migration distance. For a moderate 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:  $A = 50$ ,  $A_{\min} = 0$ ,  $s = 0.7$ .

approximation  $\psi(x) \approx \psi(0) + \psi'(0)x$ , the reproductive value

$$\mathcal{R}_d(z) \approx e^{-\delta} \{ \psi(0) + (\psi'(0) - 2)z - \psi'(0)z^2 \} \quad (3.5)$$

172 and the optimal migration distance is then

$$z^* = \max \left\{ 0, \frac{1}{2} - \frac{1}{\psi'(0)} \right\}. \quad (3.6)$$

So if the resource gradient is linear, the optimal response is to not move (be  
 174 resident) unless the dimensionless resource gradient  $\psi'(0) > 2$ , but from there, the  
 steeper the resource gradient, the farther an individual should move. Reverting to  
 176 dimensional variables, not migrating ( $z = 0$ ) is locally optimal if

$$\psi'(0) < 2fu_{\max} \quad \text{or} \quad \psi'(0) = 2fu_{\max} \quad \text{and} \quad \psi''(0) < 2fu_{\max}. \quad (3.7)$$

We can further analyze Eq. (3.4) to characterize the properties of the optima  
 178 under different conditions. By differentiating the reproductive value to identify  
 local maxima, we find  $z^*$  must solve the transcendental equation

$$Ak(1 - 2z) = 4 \cosh(k(z - s)) + 4. \quad (3.8)$$

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

$$A < \frac{4 + 4 \cosh(ks)}{k} \quad (3.9)$$

182 Heuristically, the resource cline promotes migration if it is close enough to the  
 breeding ground and large enough. Since hyperbolic cosine is convex, no more than  
 184 two interior local extreme solving Eq. (3.8) can ever coexist. Using calculus  
 techniques, we can determine that two local maxima can only coexist when

$$A > \frac{8k}{k^2 - 4}. \quad (3.10)$$

186 The bifurcation structure of the extremes of the reproductive value are  
 summarized in Figure 4. If the resource cline is weak ( $A$  is small), then the optimal

188 strategy is not to move. If the resource cline is large ( $A$  is large) and sharp ( $k$  is  
 large), then as we vary the cline position  $s$ , there will be a transitional regime  
 190 between migration and residency where 2 different local maxima will appear as the  
 cline drifts away from the breeding site (see Figure 4). In between, there is a region  
 192 where there is always a unique globally optimal movement strategy (see Figure 4).

### 3.1. Neutral resource distributions

194 The one other informative special resource distribution is the evolutionarily  
 neutral model. When directly differentiating Eq. (3.3) with respect to the  
 196 maximum migration distance, we find that at the optimum,

$$\psi'(z^*) = \frac{2}{1 - 2z^*}. \quad (3.11)$$

This ordinary differential equation has general solutions

$$\psi_{\text{neutral}}(x) := C - \ln(1 - 2x) \quad (3.12)$$

198 for any constant  $C$ . These solutions correspond to a family of perfectly neutral  
 static resource distributions. Every migration of the form of Eq. (3.2) has the same  
 200 fitness 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  
 202 a year. One of the implications of  $\psi_{\text{neutral}}(x; C)$  is that for any other static smooth  
 resource distribution  $\psi(x)$  such that  $\psi''(x) < \psi''_{\text{neutral}}(x)$ , any locally optimal  
 204 migration strategy is also globally optimal.

We show below that the neutral resource distribution is a particularly useful  
 206 idea when trying to understand how our density-independent analysis will extend  
 to density-dependent situations.

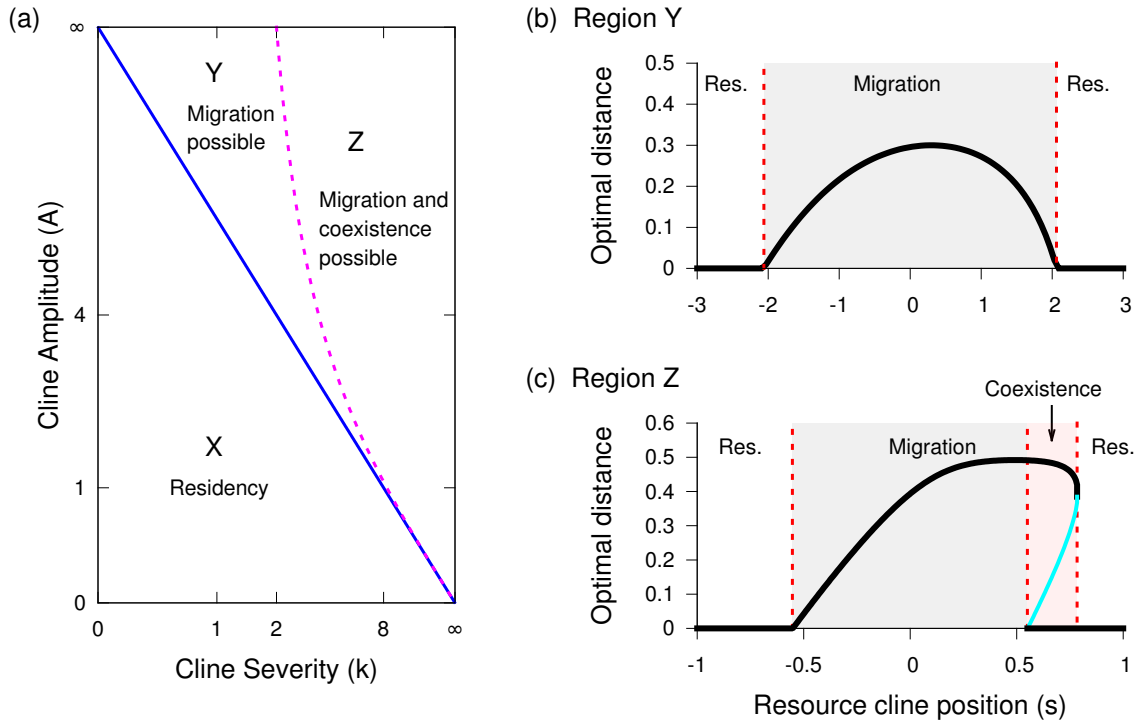


Fig. 4.— (a) The  $A \times k$  parameter space (in hyperbolic coordinates) can be dissected into 3 regions. In region  $X$ , the cost of movement always outweighs the potential resource gains, and the best strategy is reside in the breeding-ground year-round ( $x(t) = 0$  for all  $t$ ). In region  $Y$ , 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 is close to the breeding ground ( $s \approx 0$ ), the best strategy will be migration, but when the cline is far from the breeding ground ( $|s| \gg 0$ ), movement costs out-weight resource gains. In region  $Z$ , the best movement strategy still depends on the cline 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 and one saddle point. Parameter values: (b)  $A = 20$ ,  $k = 1$ ; (c)  $A = 50$ ,  $k = 10$ .

#### 4. Density-dependence

208

Although our analysis is density-independent, we can consider  
 210 density-dependent extensions of the model. For example, if migrant and resident  
 populations are regulated independently by density-dependent mortality that  
 212 occurs between breeding events (i.e. “soft” selection (Christiansen 1975; Débarre  
 and Gandon 2011)), the coexistence of migrant and resident types when the cline is  
 214 steep is preserved. On the other hand, if density-dependence acts uniformly across  
 the population (“hard” selection) or is exerted at the time of reproduction,  
 216 migrants and residents may be directly competing, and only the most fit  
 subpopulation will persist. In this particular case, individuals might increase their  
 218 reproductive success by returning to breed less often. Allowing this would not alter  
 our results. Overall, these results support previous findings (Kaitala et al. 1993)  
 220 that partial non-breeding migrations can occur without environmental  
 stochasticity, as long as density-dependent regulation of migrants and non-migrants  
 222 occurs during the non-breeding season.

If population proliferation is primarily constrained by resource depletion, then  
 224 the resource gradient will depend on the grazing pattern of the population.  
 Suppose, for example, that the resource distribution is in quasi-steady-state  
 226 equilibrium with the population. Under the pessimism principle (Mylius and  
 Diekmann 1995), the population should expand until resource supplies have been  
 228 pushed down to levels where they are just sufficient to sustain the population. This  
 level will be given by  $\max_z \mathcal{R}_d(z) = 1$ . If there are no constraints causing  
 230 inefficiency in strategy allocations, then under an ideal distribution, each strategy  $z$   
 will be used at the frequency for which  $\mathcal{R}_d(z) = 1$ .

232 The actual frequency of use of each supported strategy remains unknown. It  
 could depend on the explicit resource dynamics. Our solutions only apply to  
 234 scenarios where the resource distribution is in approximate quasi-steady-state  
 equilibrium with population densities. The problem will be much more difficult to



236 analyze when time-dynamics are considered for the resource, and may introduce  
resonance features into the evolution dynamics of migration. An example  
238 preliminary theory for such a case is provided in Appendix A, but this is a topic  
needing future exploration.

## 240 5. Discussion

Here we have used optimal control methods to exactly solve for the best  
242 movement path, given specific costs from movement and payoff from different  
resource distributions. Dimensional analysis reveals that the importance spatial  
244 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  
246 the resource distribution alone shifts whether purely migration, purely residency, or  
both are favored as the optimal movement pattern. The coexistence of movement  
248 types can be interpreted in two ways.

First, coexistence of migrant and resident types can be interpreted as partial  
250 migration, where both types occur simultaneously within the same population. Our  
model corresponds to the case of partial non-breeding migration where migrants  
252 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  
254 conditions that select on movement strategies.

Second, coexistence of migrant and resident types can be interpreted as  
256 coexistence of two species with different movement types on a single resource. In  
this case it is possible that a branching of movement types was a precursor to the  
258 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).

260 While our results provide some insight, a number of open problems remain,  
particularly with respect to the evolution of movement when populations

262 themselves alter their environments. A simple special case is proposed in Section A,  
 but even basic mathematical results for it remain unknown. Computational  
 264 experiments and mathematical analysis of spatially-explicit scenarios could greatly  
 deepen our theoretical understanding. Computational experiments could also help  
 266 us understand the relationship between the optimal strategies we’ve identified the  
 time-dependent and path-dependent aspects of evolution and speciation can lead  
 268 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  
 270 situations where adaptive responses to climate change will be more difficult.

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 sympy and scipy libraries for python (SymPy Development Team 2013; Jones et al.  
 274 2001-; Python Software Foundation 2010-). Graphics were prepared using Gnuplot  
 and Matplotlib. (Williams et al. 2010-; Hunter 2007).

### 276 A. On ideal migration allocations

As an example of migration theory where populations are constrained by  
 278 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  
 280 population using each strategy 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  
 282 and consume at a constant rate over time, the total annual grazing pressure at each  
 location  $u$  will be given by the formula

$$p(u) := \int_0^{1/2} \int_0^1 I(z) \delta(u - x(t, z)) dt dz \tag{A1}$$

284 where  $\delta()$  is Dirac’s delta-function (not to be confused with our discounting  
 parameter  $\delta$ ). Assuming individuals follow migration paths of the form of Eq. (3.2),

286 the annual grazing pressure can be simplified to

$$p(x) = (1 - 2x)I(x) + 2 \int_x^{1/2} I(z)dz. \quad (\text{A2})$$

To get further, we propose that the annual dynamics of the resource distribution  
288 are governed by the linear difference equation

$$\psi_{t+1}(x) = \max\{0, \beta\psi_t(x) + r(x) - p(x)\} \quad (\text{A3})$$

where  $\beta$  is the fraction of resource persisting from the previous season,  $r(x)$  is the  
290 annual resource inflow at all locations  $x$ , and  $p(x)$  is the annual grazing pressure  
consuming resource. Over time, the resource distribution will converge to the  
292 equilibrium

$$\bar{\psi}(x) = \max\left\{0, \frac{r(x) - p(x)}{1 - \beta}\right\}. \quad (\text{A4})$$

The reproductive success of a strategy  $z$  under a equilibrium resource distribution  
294  $\bar{\psi}$  can be determined from Eq. (3.3). So, from an allocation, we can determine the  
grazing pressure over space. From the grazing pressure, we can determine the  
296 equilibrium resource distribution. And from the equilibrium resource distribution,  
we can determine the discounted reproductive success of each strategy. Thus, the  
298 discounted reproductive success in the presence of resource depletion can be  
thought of as a function of the strategy allocation ( $\mathcal{R}_d(z; I)$ ).

300 Under the pessimism principle (Mylius and Diekmann 1995), a stable  
allocation  $I^*$  is one for which no strategy can be adopted to invade successfully  
302 ( $\max_z \mathcal{R}_d(z; I^*) = 1$ ) and no unsustainable strategy is used (for every strategy  $z$   
where  $I^*(z) > 0$ ,  $\mathcal{R}_d(z; I^*) = 1$ ). These conditions provide a set of equations from  
304 which we can attempt to identify a stable allocation  $I^*$ . General results as to when  
a stable allocation can be found, and if there are more than one for a given system,  
306 are unknown. However, using elementary fixed-point methods, we can calculate  
some elementary examples of stable allocations (see Figures 5-7).

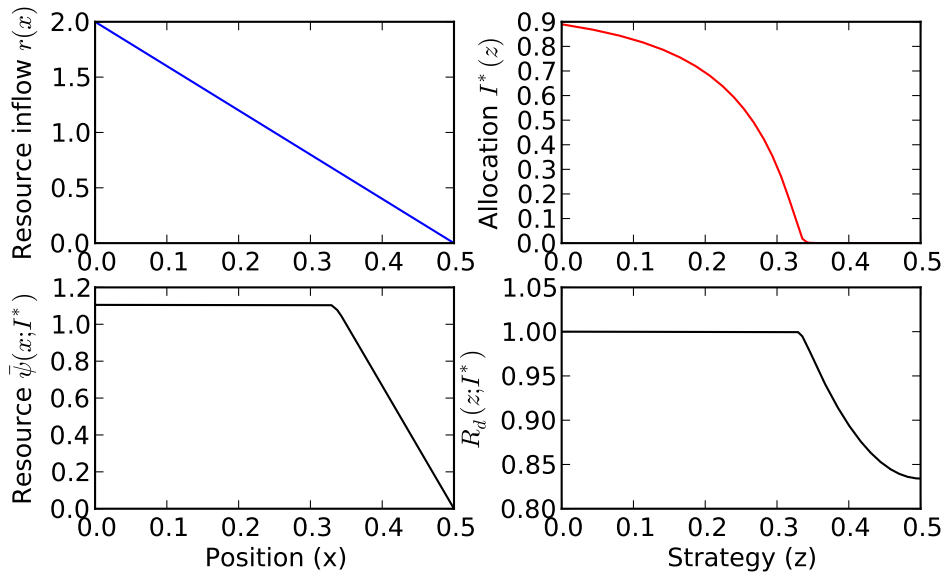


Fig. 5.— Figure of a stable strategy allocation  $I^*(z)$  when resource accumulates according to a linear gradient ( $r(x) = 2 - 4x$ ). Non-migratory strategies are the most frequently used. Parameters  $\beta = 0.4$ ,  $\delta = 0.1$ .

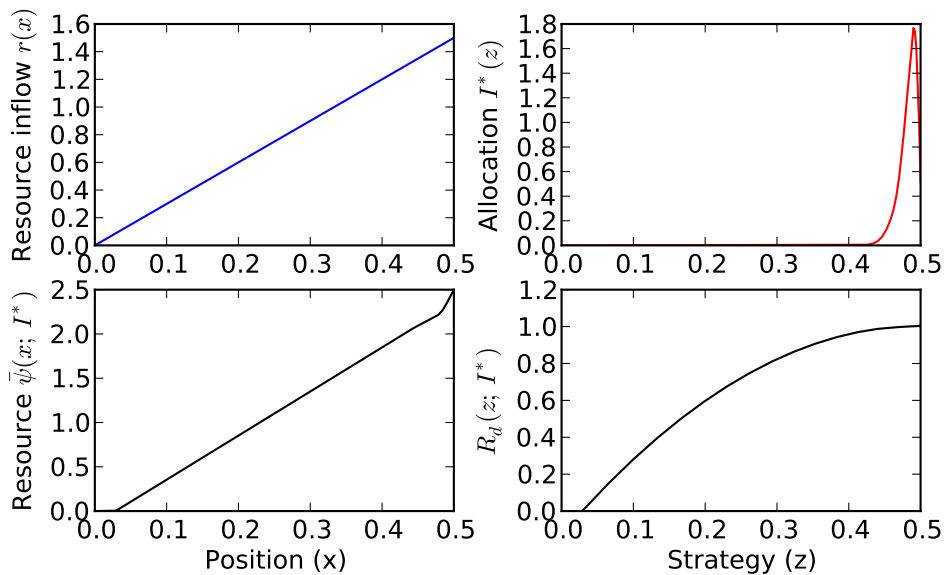


Fig. 6.— Figure of a stable strategy allocation  $I^*(z)$  when resource accumulates according to an increasing linear cline ( $r(x) = 3x$ ). The allocation is dominated by long migrations. Parameters  $\beta = 0.4$ ,  $\delta = 0.1$ .

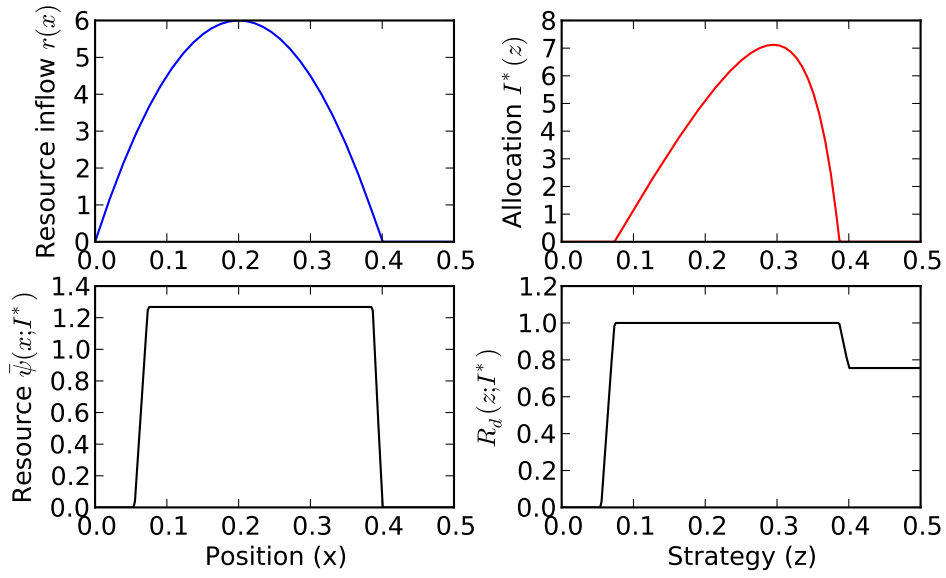


Fig. 7.— Figure of a stable strategy allocation  $I^*(z)$  when resource accumulates unimodally ( $r(x) = 60x - 150x^2$ ). Only strategies that migrate an intermediate distance are allocated. Parameters  $\beta = 0.4$ ,  $\delta = 0.1$ .

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