OPTIMAL MIGRATORY BEHAVIOR IN SPATIALLY-EXPLICIT SEASONAL ENVIRONMENTS

Timothy C. Reluga

Department of Mathematics
Penn State University
University Park, PA 16802, USA

Allison K. Shaw

Division of Evolution, Ecology, and Genetics
The Australian National University
Canberra ACT 0200, Australia
and
Department of Ecology, Evolution, and Behavior
University of Minnesota
St. Paul, MN 55108, USA

ABSTRACT. Mass migrations of vertebrate and arthropod species have long been perceived as some of the most mystical phenomena in nature. And for eons, we have been asking ourselves why animals migrate. Ecologically, migration provides benefits in currencies of survival, growth, and reproduction, allowing animals to exploit environmental heterogeneities in space and time. Yet for a given environment, different species respond with different behaviors – some travelling large distances, while others shelter in place. Part of the explanation of this distinction is the physiological differences between species and their ability to move. But is physiological difference a necessary pre-condition? Or can environmental heterogeneity itself be sufficient for bifurcations in movement behavior?

In this paper, we address this last question using a model for the evolution of migration in a density-independent, spatially-explicit setting when movement is costly based on the harvesting a single resource that varies in space and time. We use optimal control methods to calculate the optimal movement patterns in several different situations. In this framework, optimal movement strategies can be classified into six different regimes, based on the cost of movement, the strength and scale of seasonal resource variation, and the degree of trade-off between short-term and long-term benefits. We show that a migratory niche emerges in response to inseparable spatio-temporal environmental heterogeneity, and that this niche can bifurcate from changes to the resource distribution without need for physiological divergence.

1. **Introduction.** Environments change. Hazards and resources vary in both time and space, and animals only survive if they can cope with these changes. Every species seems to find its own way of coping with spatially and temporally variable environments. Strategies include dispersal and other movement, hibernation, diapause, seed-banking, randomization, delayed maturity, and energy storage [11].

Movement is a particularly interesting coping strategy displayed by all living organisms but particularly pronounced in animals. Movement allows an individual to change its position in order to avoid risks and take advantage of negative correlation in the spatial components of environmental heterogeneities. The movement patterns exhibited by any individual result from an interaction between external factors (e.g., gravity, wind, water currents), internal state (e.g., need for food, shelter, mates) and movement ability [31]. Movement can take on an impressive number of forms, varying in both temporal and spatial scales, from turbulent convection in aquatic environments over seconds to daily foraging movements to annual trips around the globe [1, 29, 30, 45]. Although external environment contributions to movement are not heritable, the mechanisms determining internal state and movement ability of an animal are heritable in part and as such, subject to natural selection. So, it is very reasonable to ask, "How do changing environments impact the evolution of movement in animals?"

This is much too large a question for a single paper, and so here, our focus will only be on the evolution of migration. Migration is defined loosely as large scale periodic movement patterns that appear to be responses to cycles of environmental variation (mostly seasonal cycles) [12]. Only a subset of species migrate [11], and it seems natural to ask, what determines whether or not a species is migratory? Clearly environmental variation plays a role, as does an individual's locomotion physiology and resource needs. Environmental heterogeneities can act to amplify existing differences between species: individuals with different characteristics will respond differently when presented with the same environment. However, to what extent can variation in environmental conditions alone drive diversification of movement strategies? This is the question we explore in this study.

While there has been a great deal of mathematical study of spatially explicit theories of movement and its evolution in stationary environments [6], far fewer studies have addressed movement in environments that vary in both space and time. We cannot say for sure why the mathematical theory has not yet addressed this topic but one factor likely contributing to the neglect is the difficulty of analyzing spatial systems with temporal forcing. It is well known that even relatively simple nonlinear forced systems like the forced pendulum and Duffing equation [22] exhibit chaotic solutions that are impossible to characterize with traditional synthetic approaches. Spatially-explicit extensions of these systems will only be more challenging.

However, the ecology of these systems describe is very important, shedding light not just on our current ecosystems, but also potentially on the ecosystems we may find on earth-like exoplanets. In this paper, we propose a spatially-explicit framework for consideration of the evolution of migration in environments that change in space and time. In section 2 we lay out a model based on the maximization of a space-time dependent fitness objective and the basic mathematical analysis using classical methods from functional calculus. In section 3 we present a preliminary analysis, and outline the results of the paper. In sections 4 and 5 we analyze a variety of specific examples in support of our general conclusions. We then close with a discussion of limitations and potential generalizations.

2. **Model.** We propose a minimal spatially-explicit model that we use to explore how seasonal environmental forcing segregates movement strategies and whether forcing alone can lead to evolutionary divergences, in the absence of physiological differences. For quick reference, the important variables of our models are summarized in Table 1. In this model, the habitat is a single non-excludable, non-rivalrous,

Table 1. Important symbols and their meanings.

Symbol	Meaning
t	Time
T	Period of seasonal oscillations
x	Position
$\dot{x}$	Velocity ($\mathrm{d}x/\mathrm{d}t$)
$\Theta(x,t)$	Resource consumption rate
$\phi(x)$	Average seasonal resource consumption.
$\omega(x,t)$	Periodic seasonal resource consumption, zero-average.
$\gamma(\dot{x})$	Rate of resource use, depending on velocity
δ	Rate of discounting future returns
u	Control variable, equal to velocity $\dot{x}$
u^*	Optimal control
$\lambda(t)$	Present value adjoint variable

in-exhaustible resource that is heterogeneously distributed in space and time. However, the resource distribution is *not* random – its distribution is predictable and periodic in time. Biologically, we assume a physiologically homogeneous population, where all individuals have the same foraging efficiency and the same profile for energy-expenditure under locomotion. Our population is structured according to periodic movement paths $x(t)$ which specify the location x of individuals at time t. The reproductive success of an individual increases linearly with increasing local resource levels. Exogenous forces cull the population in a manner independent of movement strategy so the population size is small and stable and does not impact resource abundance. If we suppose that these movement paths are perfectly heritable, then the fitness may depend on resources, as given by the total resource consumption over a lifetime minus the total resource expenditure in non-reproductive activities. Since movement incurs energy costs that increase as speed and duration increase, there is a trade-off between the costs of movement and the benefits of reaching bountiful new locations.

Reproduction occurs continuously over time, based on the current availability of resources. Let $\Theta(x,t)$ be the per-capita rate of resource consumption and reproduction at position x and time t. The resource is periodic, with period T, such that for every x,t, $\Theta(x,t) = \Theta(x,t+T)$. Let $\gamma(\dot{x})$ be the rate of resource use, depending on the current speed of movement $\dot{x}(t)$. There has been significant consideration of the mechanical and physiology trade-offs associated with efficient movement [33, 2, 16]. To avoid mathematical challenges created by more realistic formulations, we will assume the cost of movement only depends on the speed of movement ($|\dot{x}_1| = |\dot{x}_2|$ implies $\gamma(\dot{x}_1) = \gamma(\dot{x}_2)$), and not, for instance, on the direction or mass of accumulated resources.

We will use evolutionary life-history theory [40, 3] in combination with Wright's concept of fitness-landscapes [48] as our characterization of evolution. The fitness of an individual following a path $x(t)$ is given by the discounted reproduction number $\mathscr{R}_d$ [35, 43, 26] where

$$\mathscr{R}_d := \int_0^\infty \left[\Theta(x(t),t) - \gamma(\dot{x}(t))\right] e^{-\delta t} \mathrm{d}t \tag{2.1}$$

where δ represents the rate at which current reproduction is discounted relative to future reproduction because of exponential growth of the background population at rate δ. Under density-independent population growth, only individual paths with $\mathcal{R}_d > 1$ will increase in frequency over time, and strategies that maximize $\mathcal{R}_d$ will increase in frequency the most quickly.

While commonly employed, the biological foundations for this approach to evolutionary theory are not self-evident, and concerned readers may wish to jump ahead to Section 6 for critical considerations. Until then, we accept the optimization of Eq. (2.1) as our guiding definition of evolution without further comment.

Now, at any given place and time, an individual can choose the speed and direction of its movement. An individual's initial location is $x(0)$ at time $t = 0$, and changes according to $\dot{x} = u(t)$ where $u(t)$ is the chosen velocity and its movement strategy. An optimal movement strategy $u^*(t)$ will maximize the expected lifetime fitness $\mathcal{R}_d[x, \dot{x}]$, so

$$u^* = \operatorname*{argmax}_u \int_0^\infty \left[\Theta(x,t) - \gamma(u(t))\right] e^{-\delta t} \mathrm{d}t, \quad \text{when} \quad \dot{x} = u(t). \qquad (2.2)$$

One of the implications of this formulation is that any proportionate increase in the cost of movement γ can be exactly offset by a proportionate increase in the resource supply Θ. We will make use of this to simplify our model.

We can use optimal control theory [7, 24] (the modern incarnation of the calculus of variations) to calculate u^*. So far, our model formulation has been equally valid in 1, 2, or 3 dimensions, depending on our selection of spatial coordinate system. But from here on and throughout the paper, we will assume only a single spatial dimension such that $x(t)$ and $u(t)$ are scalar variables, and $\gamma(\dot{x})$ is a symmetric function. While this is certainly restrictive, it will still allow us to obtain a number of interesting results in relatively simple form.

The present-value Hamiltonian

$$\mathcal{H} = \Theta(x,t) - \gamma(u) + \lambda u. \qquad (2.3)$$

where $\lambda(t)$ is the present value adjoint variable. Then, according to the Pontryagin's maximum principle, for each t, a local optimizer of fitness $u^*(t)$ must satisfy the necessary-condition

$$u^*(t) = \operatorname*{argmax}_u \mathcal{H} = \operatorname*{argmax}_u \lambda u - \gamma(u) \qquad (2.4a)$$

subject to

$$\delta\lambda - \dot{\lambda} = \frac{\partial\Theta}{\partial x}, \quad \dot{x} = u^*. \qquad (2.4b)$$

Note that the optimal velocity $u^*(t)$ depends directly on λ, but not on x. If $\gamma(u)$ and the Hamiltonian are smooth, Eq. (2.4a) implies

$$\frac{\partial\mathcal{H}}{\partial u}(u^*) = \lambda - \gamma'(u^*) = 0. \qquad (2.5)$$

As long as $\gamma(u)$ is strictly convex and λ is not too large, there will be one and only one u^* solving Eq. (2.5). Then the updated retrograde path equations can be written as

$$\dot{x} = \gamma'^{(-1)}(\lambda), \quad \dot{\lambda} = \delta\lambda - \frac{\partial\Theta}{\partial x} \qquad (2.6)$$
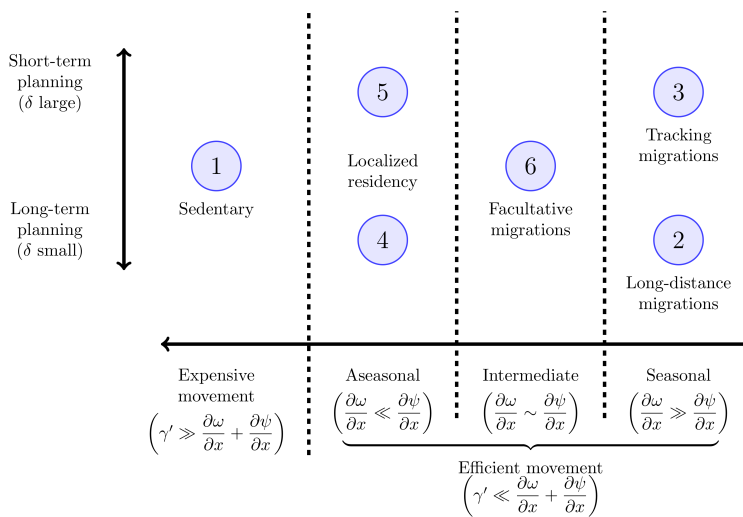
FIGURE 1. Regimes characterizing optimal movement, depending on the efficiency of movement γ', the average spatial variation in resource ($\partial\psi/\partial x$) and the periodic spatial variation in resource ($\partial\omega/\partial x$).

or equivalently, the single second-order equation

$$\gamma''(\dot{x})\ddot{x} = \delta\gamma'(\dot{x}) - \frac{\partial\Theta}{\partial x}. \tag{2.7}$$

This local weak-form condition for optimality, together with the strong form in System (2.4), are the equations around which our analysis will revolve.

Equation (2.7) by itself is not sufficient to determine the best movement strategy. In addition, we need some boundary conditions (a.k.a. transversality conditions) that are particular to the ecological circumstances under question. For our analysis, we will primarily look for cases where the path is regular and periodic over time, with a period T matching that of the seasonality, so for any solution, $x(0) = x(T)$ and $\dot{x}(0) = \dot{x}(T)$. However, other periods such as multi-annual migratory cycles [37, 39] and even non-resonant cycles [15] have been observed in nature as well and are worth considering in the future.

The reader may note at this point that the model we have constructed is only a special case of a more general theory yet to be explored. There are many other cases appropriate for a variety of ecological settings. For example, the case where animals must return to a specific location at the same time every year to reproduce, and their reproductive success is proportional to the resource accumulation over the course of the year, would lead to a different but related set of equations (Reluga and Shaw, in submission). This framework has the potential to be useful for understanding movement patterns beyond seasonal migration, although this would result is a more complicated model as most non-migratory movement is not periodic.

3. **Preliminary analysis.** Optimization theory allows us to describe some possible end results of the evolution of movement behaviors. It does not allow us to

investigate the evolution of behavior directly, or through related factors like environmental cues, social cues, learning, memory, and instinct. Even independent of physiological demands, the fitness landscape over which migration must evolve may be very rough and evolutionary optima may be inaccessible.

As long as the resource distribution is a nicely behaved function, it can be uniquely decomposed into constant and periodic components, such that

$$\Theta(x,t) = \psi(x) + \omega(x,t) \tag{3.1}$$

where

$$\psi(x) := \frac{1}{T} \int_0^T \Theta(x,t)\mathrm{d}t \quad \text{and} \quad \omega(x,t) := \Theta(x,t) - \psi(x). \tag{3.2a}$$

The periodic component $\omega(x,t)$ can be expanded further with Fourier series such that

$$\omega(x,t) = \sum_{n=1}^{\infty} \left[\alpha_n(x) \sin\left(\frac{2\pi nt}{T}\right) + \beta_n(x) \cos\left(\frac{2\pi nt}{T}\right) \right] \tag{3.2b}$$

$$\alpha_n(x) := \frac{2}{T} \int_0^T \Theta(x,t) \sin(2\pi nt/T)\mathrm{d}t \tag{3.2c}$$

$$\text{and} \quad \beta_n(x) := \frac{2}{T} \int_0^T \Theta(x,t) \cos(2\pi nt/T)\mathrm{d}t. \tag{3.2d}$$

Unless otherwise stated, we will choose our time units such that $T = 1$.

We may reinterpret Eq. (2.7) as

$$\left(\frac{\mathrm{d}\ln \gamma'(\dot{x})}{\mathrm{d}t} - \delta\right)\gamma'(\dot{x}) = -\frac{\partial\psi(x)}{\partial x} - \frac{\partial\omega(x,t)}{\partial x}. \tag{3.3}$$

This suggests that there are 4 competing components which characterize the nature of optimal movement strategies. These parameters are the amplitude of spatial variation in resource availability, which is decomposed into the average resource level (ψ) and the seasonal resource variation (ω), the efficiency of movement (γ'), and the relative importance of short-term resource gains verses long-term gains (δ).

One observation is that if spatial and temporal variation are independent and additively separable (so $\Theta(x,t) = \psi(x) + \omega(t)$), then seasonality does not affect optimal movement. Another is that velocity only appears through $\gamma'(\dot{x})$ with units of cost per unit of distance, indicating the potential scales of spatial movement are limited by the efficiency of movement. Taking this a step further, optimal movement strategies can be classified into six regimes based on the relative sizes of these components (see Figure 1). If movement is inefficient, relative to the amplitude of spatial resource variation, there is no benefit to moving (regime 1) and the species will be sedentary, without aggregation. If the movement cost is small, then movement offers advantages to improve fitness. When movement is efficient and seasonal resource variation is large compared to stationary variation, then the optimal movement strategy will be to pursue seasonal increases in resource availability. If short-term gains are most important, the optimal strategy will be the pursuit of resource gradients, and there may be many regional non-overlapping migrations separated by resource deserts (regime 3). If long-term gains dominate in importance, there will be a unique optimal migration path, potentially crossing resource deserts over long distances (regime 2). When movement is efficient and seasonal resource variation small compared to stationary variation, then the optimal movement
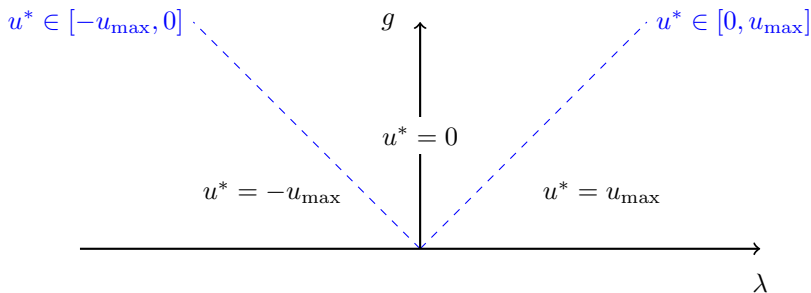
FIGURE 2. Diagram of the segmentation of $u^*(\lambda, g)$, the velocities that maximize the Hamiltonian, depending on the shadow price λ when $\gamma(u) = g|u|$.

strategy will be to move to local resource peaks and become resident there. If short-term resource needs dominate long-term resource needs, then the best strategy is to climb the resource gradient to the nearest local maximum (regime 5). The lower the discount rate, the greater the importance of long-term resource gains, and the more advantageous it is to cross resource deserts to become resident at the global resource maximum (regime 4). When seasonal variation is similar in size to the average variation (regime 6), the structure of optimal solutions can be very complex and there is no simple periodic movement that provides a clear fitness maximizer. In this situation, facultative migrations that respond to particular conditions may be better strategies. In the following sections, we will provide examples of each of these.

4. **Piecewise linear movement costs.** To begin our exploration, we consider the special limiting case of a piecewise-linear movement-cost function. Let

$$\gamma(u) = \begin{cases} g|u| & \text{if } |u| \leq u_{\max}, \\ \infty & \text{otherwise.} \end{cases} \tag{4.1}$$

This family of movement cost functions is special, in that it contains the least convex of all admissible possibilities. Since this $\gamma(u)$ is not differentiable, though, we must work with the strong form of our optimality condition (Eq. (2.4)) in our analysis. The optimal velocity can be determined in piecewise form (see Figure 2).

$$u^*(\lambda, g) = \operatorname*{argmax}_{u} \mathcal{H} = \begin{cases} u_{\max} & \text{if } \lambda > g, \\ [0, u_{\max}] & \text{if } \lambda = g, \\ 0 & \text{if } -g < \lambda < g, \\ [-u_{\max}, 0] & \text{if } \lambda = -g, \\ -u_{\max} & \text{if } \lambda < -g. \end{cases} \tag{4.2}$$

One immediate consequence of Eq. 4.2 is that every optimal migration pattern must contain periods of residence, where there is no movement. Since periodic movement requires both positive and negative velocities, and λ varies continuously, we always have to pass through intervals of $u^* = 0$.

4.1. **Regime 1: Expensive movement.** Consider now a situation where a habitat has a single resource peak with a location that oscillates back and forth seasonally. Making use of only the first terms of our Fourier expansion, and assuming symmetry for mathematical convenience, let us postulate

$$\Theta(x,t) = a_0 - \frac{a_2}{2}x^2 + a_1 \sin(2\pi t)x, \tag{4.3}$$

with $a_2 > 0$ and attempt to find exact periodic solutions of Eq. (2.4).

$$\delta\lambda - \dot\lambda = a_1 \sin(2\pi t) - a_2 x, \quad \dot x = u^*(\lambda). \tag{4.4}$$

Without loss of generality, we can rescale our dimensions taking $\hat\lambda = g\lambda$, $\hat x = u_{\max}x$, $\hat a_1 = ga_1$, $\hat a_2 = ga_2/u_{\max}$, such that $g = 1$ and $u_{\max} = 1$.

We solve Eq. (4.4) in pieces, making use of the constancy of u^*. Over any interval where the speed is constant, $x(t) = (t - \tau)u^* + x(\tau)$ and

$$
\begin{aligned}
\lambda(t) - \lambda(\tau)e^{\delta(t-\tau)} &= \frac{a_1\left[\delta\sin(2\pi t) + 2\pi\cos(2\pi t)\right]}{\delta^2 + 4\pi^2} \\
&\quad - \frac{a_1\left[\delta\sin(2\pi\tau) + 2\pi\cos(2\pi\tau)\right]e^{\delta(t-\tau)}}{\delta^2 + 4\pi^2} \\
&\quad + \frac{a_2\left[\delta(\tau-t)u^* + (u^* + \delta x(\tau))\left(e^{\delta(t-\tau)} - 1\right)\right]}{\delta^2}
\end{aligned} \tag{4.5}
$$

where $(x(\tau), \lambda(\tau))$ is an arbitrary point on the solution. While $\lambda(t) > 1$, $u^* = 1$, while $\lambda(t) < 1$, $u^* = -1$, and while $\lambda(t) \in (-1, 1)$, $u^* = 0$.

When looking for stationary solutions with $u^* = 0$, $x(t) = x(\tau)$. This can only stay stationary as long as $-1 < \lambda < 1$. First, this implies that there can not be any exponential growth, so we must have

$$\lambda(\tau) = \frac{a_1 \sin(2\pi\tau + f(\delta))}{\sqrt{\delta^2 + 4\pi^2}} - \frac{a_2 x(\tau)}{\delta}, \quad \text{where} \quad f(\delta) = \text{Asin}\left(\frac{2\pi}{\sqrt{\delta^2 + 4\pi^2}}\right). \tag{4.6}$$

Second, since after substitution of $\lambda(\tau)$ into Eq. (4.5), we now have

$$\lambda(t) = \frac{a_1 \sin(2\pi t + f(\delta))}{\sqrt{\delta^2 + 4\pi^2}} - \frac{a_2 x(\tau)}{\delta}, \tag{4.7}$$

we can only keep $u^* = 0$ for all time provided the extreme values of $\lambda(t)$ given by

$$\frac{\pm a_1}{\sqrt{\delta^2 + 4\pi^2}} - \frac{a_2 x(\tau)}{\delta} \in [-1, 1]. \tag{4.8}$$

All periodic solutions with constant position must satisfy

$$|x(\tau)| \le \frac{\delta}{a_2}\left(1 - \frac{a_1}{\sqrt{\delta^2 + 4\pi^2}}\right). \tag{4.9}$$

No periodic solution will have $x(t) = x(\tau)$ everywhere unless (in dimensional variables)

$$\left(\frac{a_1}{g}\right)^2 < 4\pi^2 + \delta^2. \tag{4.10}$$

If movement is too inefficient relative to seasonal variation in resource availability, or the discount rate of returns is too large, the optimal strategy is to be sedentary instead of migratory (regime 1).

In cases where seasonal variation is sufficiently strong, we can construct optimal movement patterns using numerical or semi-analytic methods (see Figure 3). Our
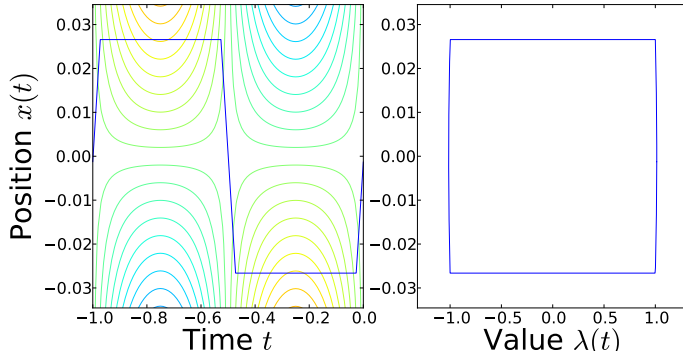
FIGURE 3. An example time series (left) and phase-plane (right) plots of an optimal limit cycle when the cost of movement is given by Eq. (4.1) and the resource distribution (colored curves) is given by Eq. (4.3). The path moves when in areas of low resource, and stops when in areas of sufficiently high resource. Parameter values $\delta = 0.05$, $a_2 = 0.2$, $a_1 = 6.38$. We note that this figure has a strong similarity to diagrams of arctic tern migration [1](Figure 1).

analyses for piecewise linear costs indicate that there is a unique solution with period 1 for any a_2, as long as movement is not expensive relative to the variation in resource distribution, i.e. $\left(\dfrac{a_1}{g}\right)^2 > 4\pi^2 + \delta^2$. However, the process of demonstrating this seems tedious and opaque, potentially incorporating singular trajectories, so instead of pursing this further, we move on to a mathematically friendlier class of examples.

5. **Parabolic movement costs.** The simplest available alternative to piecewise linear movement costs which do not have corners seems to be parabolic costs. If

$$\gamma(u) := gu^2/2, \tag{5.1}$$

then $\gamma'(u) = gu$, $\gamma''(u) = g$. Under the hypothesis of parabolic costs, Eq. (2.7)'s retrograde path system is

$$\dot{x} = \frac{\lambda}{g}, \quad \dot{\lambda} = \delta\lambda - \frac{\partial\Theta}{\partial x}. \tag{5.2}$$

Written as a single equation,

$$\ddot{x} = \delta\dot{x} - \frac{1}{g}\frac{\partial\Theta}{\partial x}. \tag{5.3}$$

As observed above, increases in movement cost can be offset by increases in resource supply. When the movement cost parameter g is absorbed into our parameterization of the resource abundance Θ, then, it suffices to consider

$$\ddot{x} = \delta\dot{x} - \frac{\partial\Theta}{\partial x} \tag{5.4}$$

as a necessary condition for optimality. The convenience of the parabolic-costs postulate loses us some realism. In particular, the parabolic-costs postulate proposes that slow-movement is essentially free, and there is no upper bound on movement

velocity. As we have already seen, correction of this leads to situations where movement stops.

If we go one minor step further, and reverse time, so $t = -\tau$, we then have a classical model of damped nonlinear vibrations. There is a large body of literature on nonlinear vibrations, including special cases of Eq. (5.4) corresponding to the harmonic oscillator, Duffing equation, Hill equation, and Mathieu equation, all with forcing and damping [32, 44]. However, mechanical stability, dissipation, and potential energy minimization lead most of these studies to neglect the situations needed here, where solutions are not locally stable.

5.1. **Regimes 2 and 3: Migration under strong seasonality.** If we return to considering a habitat dominated by a single-peaked resource and a seasonally varying linear gradient, given by Eq. (4.3), the path equation under parabolic costs, Eq. (5.4), becomes an anti-damped, forced harmonic oscillator

$$\ddot{x} = \delta \dot{x} - a_1 \sin(2\pi t) + a_2 x. \tag{5.5}$$

In this case, solutions can be fully calculated using standard methods from undergraduate differential equations. There is exactly one periodic solution, given as

$$x(t) = \frac{a_1 \left[(a_2 + 4\pi^2) \sin(2\pi t) - 2\pi\delta \cos(2\pi t) \right]}{(a_2 + 4\pi^2)^2 + (2\pi\delta)^2} = \frac{a_1 \sin(2\pi t - F(a_2, \delta))}{\sqrt{(a_2 + 4\pi^2)^2 + (2\pi\delta)^2}} \tag{5.6}$$

where $F(a_2, \delta) = \mathrm{Asin}\left(2\pi / \sqrt{(a_2 + 4\pi^2)^2 + (2\pi\delta)^2} \right)$ is a non-negative phase-shift. In the limit of slow discounting ($\delta = 0$),

$$x(t) = \frac{a_1 \sin(2\pi t)}{a_2 + 4\pi^2}. \tag{5.7}$$

Example periodic movement trajectories, with resource supply, are shown in Figure 4.

From this solution we see that the migration distance increases as the amplitude of seasonal resource variation increases, but decreases as the discount rate or parabolic curvature increase. We also see that the phase-shift of the optimal path is determined by the discounting of future resource collection. The stronger discounting, the more the individual should follow the current resource gradient (regime 3). In the case of very large discounting,

$$\frac{\mathrm{d}x}{\mathrm{d}t} \propto -\frac{\partial\Theta}{\partial x}. \tag{5.8}$$

On the other hand, the less discounting, the more the individual moves in anticipation of future resource changes (regime 2) so that they never have fewer resources available than if they had stayed at $x = 0$.

5.2. **Regimes 4 and 5: Aseasonality and residency.** If seasonal contributions to resource availability are weak or absent ($\omega(x, t) = 0$), the resource distribution can be approximated by its stationary part $\psi(x)$. Then our intuition tells us that optimal strategies should correspond to residing at peaks in the resource distribution. When the resource distribution is stationary and independent of time, Equation (5.4) is a second-order autonomous equation that can be studied in the phase-plane.
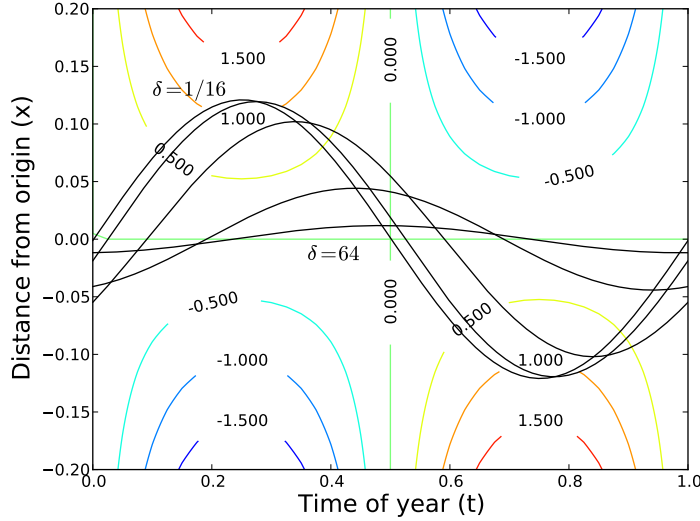
FIGURE 4. Example of periodic movement paths for Eq. (5.6), for discount rates $\delta = 1/16, 1, 4, 16, 64$. Colored curves show a contour plot of resource supply $\Theta(x, t)$ given by Eq. (4.3) with $a_0 = 0$, $a_1 = 30/\pi$, and $a_2 = 10^{-6}$. As the discount rate increases, migration is reduced, and the phase shifts toward a myopic, greedy behavior.

If the resource distribution of the habitat has a single resource peak, something like $\psi(x) := a_0 - a_2 x^2$, then $x = 0$ is the peak, $\psi' = -2a_2 x$, and our first-derivative condition Eq. (5.4) implies that along an optimal path,

$$\ddot{x} = \delta\dot{x} + a_2 x. \tag{5.9}$$

The exact solutions of this are elementary,

$$x(t) = C_1 e^{\frac{\delta + \sqrt{\delta^2 + 4a_2}}{2}t} + C_2 e^{\frac{\delta - \sqrt{\delta^2 + 4a_2}}{2}t}. \tag{5.10}$$

The only case where this is a periodic function is the case where $C_1 = C_2 = 0$, and $x(t) = 0$. Thus, the globally-optimal movement strategy is to remain at the resource peak forever and to never move, regardless of the specific parameter values. If an individual starts at some location $x(0) \neq 0$, the optimal approach to the resource peak is determined by setting $x(\infty) = 0$, and is given by

$$x(t) = x(0)e^{\frac{\delta - \sqrt{\delta^2 + 4a_2}}{2}t} \tag{5.11}$$

The optimal velocity in feedback form for approaching the stationary solution is

$$\dot{x} = \left(\frac{\delta - \sqrt{\delta^2 + 4a_2}}{2}\right)x. \tag{5.12}$$

When there are multiple peaks in the resource, this model allows for multiple points that are locally best. For instance, if
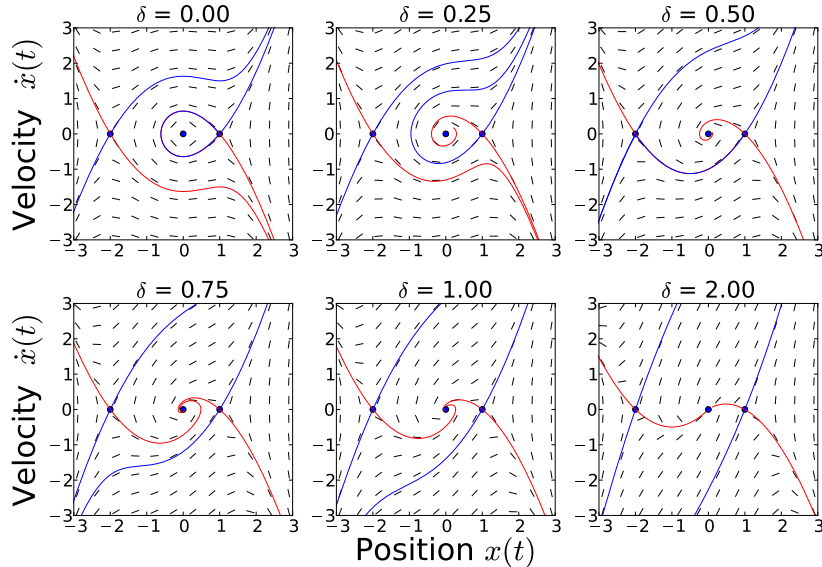
$$\psi(x) = a_0 - a_2 x^2(3x^2 + 4x - 12), \tag{5.13}$$

FIGURE 5. Phase-plane plots of the solutions of Eq. (5.4) when $\Theta(x, t)$ is given by Eq. (5.13), with $a_0 = 0$, $a_2 = 1$. Red curves and blue curves are the stable manifolds and unstable manifolds of the saddle points respectively. (the central stationary point is always a center, unstable focus, or unstable node) If the discount rate (δ) is very high, the optimal strategy is to chase the gradient. Decreased discounting can lead to a situation where there is ambiguity in the best action around the minimum. This ambiguity is always present for smaller discount rates, and its domain grows as the morality rate decreases. If the discount rate is smaller than than needed for a heteroclinic connection, there is always an initial condition that leads to the global maximum.

there are two local maxima in the resource distribution, $x = 1$ and $x = -2$, both of which are reached under optimizing strategies from some initial positions, although $\psi(-2) = a_0 + 32a_2$ dominates $\psi(1) = a_0 + 5a_2$ globally. Phase-plane solutions are shown in Figure 5. Note that while $x = \dot{x} = 0$ is a stationary point, it is not a fitness maximum. This is a general issue in the analysis of optimal movement, based on Eq. (2.7) – any optimal movement path under our hypotheses will satisfy this equation, but not everything that satisfies the equation has to be optimal – other solutions may correspond to minima or saddle points, and in some cases, optimal solutions may not exist. Sufficient conditions for the optimality of movement paths are much harder to make use of in variational calculus as they are in regular single-variable calculus, so we do not rigorously address this issue.

Clearly, there is no need for periodic migration in this habitat. Extensions of this situation have been heavily studied, particularly in the density-dependent case where individuals can incorporate random-movement components within their strategy. This had recently lead to the particular success with ideal free distribution theory [13, 4, 5], including extensions that incorporate movement costs [10].

What is most interesting when considering a habitat with multiple resource peaks, is not so much the stationary strategies, but the basins of convergence to

these strategies, which are controlled by the degree of discounting between short-term and long-term returns. An optimal path from $x = 1$ to $x = -2$ only exits when $\delta < \sqrt{a_2}/2$. When long-term returns are heavily discounted, solutions pursue the local gradients to the nearest resource maxima (regime 5). But when discounting is low, the basins of attraction to local maxima begin to overlap, with different initial beliefs about the value of future returns (λ) leading to different maxima. Eventually, heteroclinic orbits form, and transient solutions can enable movement from a small resource maximum to a larger resource maximum. Without any discounting of future returns, there exist optimal paths from anywhere to the global resource maximum (regime 4).

5.3. **Regime 6: Intermediate seasonal variation.** Having now seen cases with weak and strong seasonal variation, it is natural to consider cases where the strength of seasonal variation is too strong to be ignored, but too weak to dominate average spatial variation. One example is the bimodal resource distribution plus a seasonal gradient, such as

$$\Theta(x, t) = a_0 + a_2 x^2 - a_4 x^4 + a_1 \sin(2\pi t)x, \qquad (5.14)$$

with all $a_i > 0$. Under the parabolic cost assumption, then, an optimal path must satisfy

$$\ddot{x} = \delta \dot{x} - a_1 \sin(2\pi t) - 2a_2 x + 4a_4 x^3, \qquad (5.15)$$

an equation widely known as the Duffing equation [22]. The Duffing equation has been studied extensively in the applied mathematics literature since 1918 as an example of a forced nonlinear oscillator. Often, these analyses have focused on parameter regimes that are more relevant for mechanics than ecology. While some papers do consider this double-well regime [23, 42], these analyses are "upside-down" with $a_2 < 0$ and $a_4 < 0$. Still, we can glean a few basic ideas about the solution structure. There is a global unique periodic solution when seasonality is strong (a_1 is large), and two periodic solutions localized to the neighborhoods of the resource peaks when seasonality is weak (a_1 is small). However, the transition between these two regimes is very complicated. For some parameter values, the dynamics are chaotic, and no simple periodic solution can be found that characterizes the best way to move between the two resource peaks. For other parameter values, the smaller-scale peak-localized periodic paths can co-exist with larger between-peak periodic paths.

Use of the Duffing equation as a standard model presents an extra challenge when we turn it right-side up for migration analysis – most solutions blow-up in finite-time. This encourages one to look for alternatives that are better behaved, and indeed there are several to choose from. One that seems particularly attractive is to extend the forced harmonic potential (4.3) to include two stationary symmetric local resource peaks, so

$$\Theta(x, t) = a_0 - \frac{a_2}{2}x^2 + a_1 \sin(2\pi t)x + B \left(e^{\frac{-(x+1)^2}{\sigma^2}} + e^{\frac{-(x-1)^2}{\sigma^2}} \right) \qquad (5.16)$$

The peaks have been chosen to center at ± 1, but this can be changed by rescaling space.

The analysis of the necessary condition resulting from Eq. (5.16) is challenging, and is probably best undertaken numerically for parameter values corresponding to
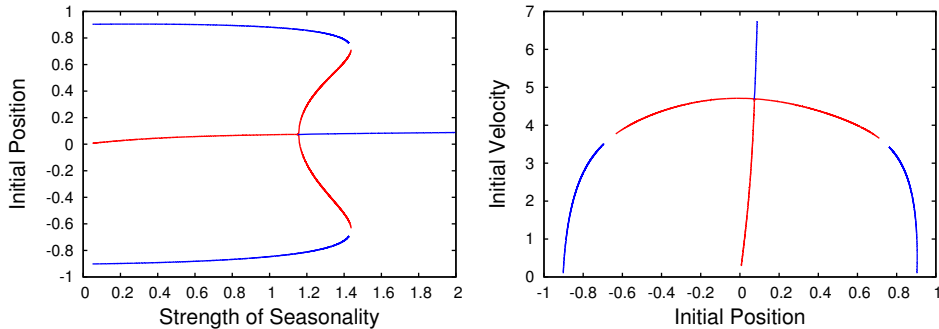
Figure 6. Example bifurcation diagram for a seasonally oscillat-
ing parabolic resource with two symmetric fixed resource peaks,
as described by Eq. (5.16). At left, we show the initial positions
of period-1 solutions depending on the strength of seasonality, as
specified by the amplitude parameter a_1. At right, we plot the full
initial conditions of periodic solutions for all amplitudes. Saddle
points are plotted in blue. When seasonality is weak, there are
period-1 solutions on each peak, with a spurious periodic solution
in the middle. For strong seasonality, there is a single maximizing
periodic solution. For intermediate seasonality ($1.15 < a_1 < 1.43$),
resident and long-distance migratory local optimal co-exist. As the
strength of seasonality increases, the initial velocity also tends to
increase. Parameter values $\delta = 0.5$, $B = 20$, $\sigma = 1.1$, $a_2 = 0.02$.
The small gaps between the ends of the red and blue curves are
due numerical difficulties near the bifurcation points.

regime 6. Numerical studies confirm our expectation that the structure of optimiz-
ing solutions will not be simple for intermediate seasonal variation (see Figures 6
and 7). We see regionally localized movement for weak seasonality, a single large
migration for strong seasonality, and set of bifurcations (pitchfork and two fold
bifurcations) for intermediate strength forcing. This suggests that there may be
abrupt jumps in the evolution of movement as the strength of seasonality slowly
varies over time, and that costly movement combined with spatial-temporal het-
erogeneity can indeed partition a niche without physiological adaptation being a
prerequisite.

Our observations suggest that more complex strategies may offer advantages in
regime 6 when seasonality is strong and discounting is slow. For example, even
though explanations of partial migration based on game-theory models [21, 8, 25]
do not apply in our framework because of our theory is density-independent, mixed-
strategy-like randomized strategies with multi-year periods may out-complete be-
haviors with a period of 1 year. They reduce risk by smoothing a rough fitness
landscape and enhancing the potential for rescue effects. This appears to be the
case in Bristol Bay salmon [36], where life history diversity makes the migrating
populations resilient against environmental disturbances.

6. **Discussion.** Here we have used methods from optimal control theory to study
the question: can environmental heterogeneity alone drive diversification of move-
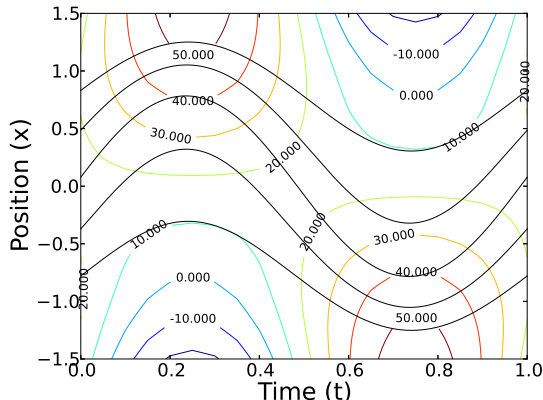ment strategies? Optimal movement patterns in our model can be classified into

FIGURE 7. Plot showing the 5 period-1 solutions of Eq. (5.16) when $a_1 = 1.31$. The top, middle, and bottom ones seem to correspond to local fitness maxima. Other parameter values same as Fig. 6.

six regimes based on the relative values of four model parameters (time-averaged spatial resource variation, seasonal resource variation, movement efficiency, and the relative importance of short versus long term gains).

Given how extensive migration research is, there exist surprisingly few general models aimed at understanding the ecological conditions that drive animal migration [14]. Most such models have essentially asked the Clash question of "should I stay or should I go" and considered the discrete decisions of migrating or not. For example, Wiener and Tuljapurkar [46] showed that negative correlation in resources between two patches favors migration between them. Holt and Fryxell [18] derive conditions favoring residency in single environment or migration between two, in a model with no cost to movement.

However, in reality there is a gradient of different movement types and since migration in particular is an adaptive response to resources that are heterogeneously distributed in space and time [9] spatially-explicit models provide a perspective that is lacking in spatially-implicit ones [38]. Our work builds on existing theory by presenting an analytic/numerical analysis of migration patterns in a spatially-explicit environment. Our results are completely classical, and we are somewhat surprised that they seem to be absent from the theoretical ecology literature still.

We find that one key condition for the emergence of migratory behavior is the coupling of spatial and temporal heterogeneities. This fits with past descriptions of different movement or behavioral patterns as occurring within a space-time framework *e.g.* [11, 29]. This result is also consistent with other theoretical findings [17] that studies of separable heterogeneities are insufficient to explain ecological dynamics.

In our analysis, we have used several simplifying assumptions: that reproduction is uncorrelated to space or time, that reproductive success is density-independent, that there is no age structure, that there are no other life-history constraints, that movement only occurs in a single spatial dimension, that there are no cognitive constraints on movement behavior, that the efficiency of movement is constant,

that there is a single inexhaustible resource of importance, and that the environment exhibits no randomness in space or time. These assumptions are all approximations, for which the accuracy depends on the circumstances of the application of interest.

The density-independent factors of life-history, movement mechanisms, and resource-dependent reproduction, are presented in only their simplest possible forms to allow for a concise theory, and while we can elaborate the mathematics to incorporate more specific definitions, we do not expect these to invalidate our results. When extending our analyses from one dimension to two or three dimensions, we expect to find a greater variety of locally-optimal solutions. This theory has no means of accounting for density-dependent factors, whether they occur via reproduction, direct competition, or resource-mediated competition. Such factors will need to be introduced into the theory, perhaps by extending the density-dependent patch models of Holt and Fryxell [18], if we are to understand which strategies that are sub-optimal under density-independent theory become competitive because of density-dependent resource pressures.

Fitness landscapes like the one we postulate in Eq. (2.1) provide useful conceptual tools for characterizing trends in natural selection, but their mechanistic underpinnings in theoretical biology are somewhat questionable. There are a number of issues that can be discussed, but perhaps the most important factor here is that spatial segregation of strategies by definition eliminates the competitive exclusion principle upon which "the struggle for survival" is premised. In our density-independent theory, optimal strategies may come to dominate population statistics when data-sampling is performed in a location-independent manner. But spatially localized sampling will reveal persistence of "sub-optimal" migration strategies indefinitely. An interesting future project would be the development of a density-dependent quasi-species theory that could predict the distribution of persistent strategies across the population.

Extensions of our theory that allow for competition between strategies, perhaps by accounting for range-overlaps due to noisy components of migration, may help shed light. The fact that simulation models allowing competition between strategies have found results similar to some of ours [38], suggests that these extension will not invalidate our overall findings but instead serve to provide a deeper understanding of biological mechanisms favoring different movement strategies. It should be possible to use stochastic-process methods to determine the best behaviors in situations where the environment is periodic but movement exhibits random effects using diffusion theory by studying

$$\mathscr{R}_d = \int_x \int_0^\infty e^{-\delta t} \left[\Theta(x(t), t) - \gamma(u(x(t), t))\right] \mathrm{d}t \mathcal{D}x$$

$$\text{where} \quad \mathrm{d}x = u(x, t)\mathrm{d}t + \sigma(x, t)\mathrm{d}W. \quad (6.1)$$

This leads to a present-value Hamiltonian

$$\mathscr{H} = \int_{-\infty}^\infty [\Theta(x, t) - \gamma(u(x, t))]p(x, t)dx + \int_x V(x, t) \left(u\frac{\partial p}{\partial x} + \frac{\sigma^2}{2}\frac{\partial^2 p}{\partial x^2}\right) \mathrm{d}x \quad (6.2)$$

where adjoint value

$$V(y, t) = \int_{y=x(t)} \int_t^\infty e^{-\delta s}[\Theta(x, s) - \gamma(u(x, s))]\mathrm{d}s \mathcal{D}x. \quad (6.3)$$
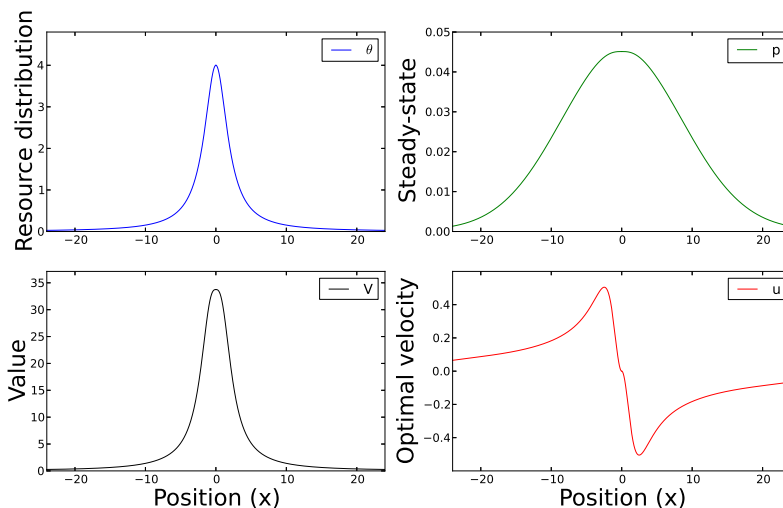
FIGURE 8. Example calculation of a steady-state solution of System (6.4) when $\Theta(x,t) = 16/(4 + x^2)$, $\gamma = u^2/2$, and $\sigma = \sqrt{2}$, and $\delta = 1/10$. The largest advection speeds occur when individuals are close to, but not at, the resource peak.

This leads, by functional calculus methods, to the necessary conditions

$$\frac{\partial p}{\partial t} = u^* \frac{\partial p}{\partial x} + \frac{\sigma^2}{2} \frac{\partial^2 p}{\partial x^2}, \tag{6.4a}$$

$$\delta V - \frac{\partial V}{\partial t} = -\frac{\partial(u^* V)}{\partial x} + \frac{\sigma^2}{2} \frac{\partial^2 V}{\partial x^2} + \Theta(x,t) - \gamma(u^*), \tag{6.4b}$$

$$p\gamma'(u^*) = V\frac{\partial p}{\partial x}. \tag{6.4c}$$

For a periodic environment, we have the further boundary conditions $p(x,t) = p(x,t+T)$, $V(x,t) = V(x,t+T)$. In the steady-state case, these coupled partial differential equations reduce to a system of 4 first-order ordinary differential equations that can be solved numerically (see Figure 8).

Another approach to consider is the use of weak periodic perturbations of existing diffusive ideal free distribution models. It would be quite interesting as well to explore the relationships between our approach and the circuit-theory of movement which is premised on spatially-dependent movement costs, in contrast to our spatially-independent movement costs [27].

In environments where strong random fluctuations affect fitness or movement, our methods and results will certainly not be helpful – all our mathematics assumes the future is precisely predicted. When the environment is itself random, individuals will need to adopt some heuristic decision process, and the specifics of this heuristic process may have very large consequences for observed migration patterns. Even in the periodic scenarios we examine here, specifics of cognitive processes may prevent the best migration pattern from being achieved.

Our work highlights a number of areas in need of more research, which we hope will be explored by future studies.

REFERENCES

[1] T. Alerstam, A. Hedenström and S. Åkesson, Long-distance migration: Evolution and determinants, *Oikos,* **103** (2003), 247–260.

[2] R. M. Alexander, When is migration worthwhile for animals that walk, swim or fly?, *Journal of Avian Biology,* **29** (1998), 387–394.

[3] M. Bulmer, *Theoretical Evolutionary Ecology*, Sinauer, Sunderland, MA, 1994.

[4] R. S. Cantrell, C. Cosner, D. L. Deangelis and V. Padron, The ideal free distribution as an evolutionarily stable strategy, *Journal of Biological Dynamics,* **1** (2007), 249–271.

[5] R. S. Cantrell, C. Cosner and Y. Lou, Approximating the ideal free distribution via reaction-diffusion-advection equations, *Journal of Differential Equations,* **245** (2008), 3687–3703.

[6] S. Cantrell, C. Cosner and Y. Lou, Evolution of dispersal in heterogeneous landscapes, in *Spatial Ecology* (eds. S. Cantrell, C. Cosner, and S. Ruan), Chapman and Hall, (2009), 213–229.

[7] C. W. Clark, *Mathematical Bioeconomics*, John Wiley & Sons, Inc., Hoboken, NJ, 2010.

[8] D. Cohen, Optimization of seasonal migratory behavior, *American Naturalist*, **101** (1967), 5–17.

[9] K. A. Cresswell, W. H. Satterthwaite and G. A. Sword, Understanding the evolution of migration through empirical examples, in *Animal migration: A synthesis, Oxford University Press,* New York, ISBN 978-0199569007, (2011), 7–16.

[10] D. L. DeAngelis, G. S. Wolkowicz, Y. Lou, Y. Jiang, M. Novak, R. Svanbäck, M. S. Araujo, Y. S. Jo and E. A. Cleary, The effect of travel loss on evolutionarily stable distributions of populations in space, *The American Naturalist,* **178** (2011), 15–29.

[11] H. Dingle, Ecology and evolution of migration, in *Animal migration, orientation and navigation* (ed. S. A. Gauthreaux), (1980), 1–101.

[12] H. Dingle and V. A. Drake, What is migration?, *Bioscience,* **57** (2007), 113–121.

[13] S. D. Fretwell and H. L. Lucas, On territorial behavior and other factors influencing habitat distribution in birds, *Acta Biotheoretica,* **19** (1969), 37–44.

[14] J. M. Fryxell, E. Milner-Gulland and A. R. Sinclair, Introduction, in *Animal migration: A synthesis,* Oxford University Press, New York, ISBN 978-0199569007, (2011), 1–3.

[15] N. J. Gales, A. J. Cheal, G. J. Pobar and P. Williamson, Breeding biology and movements of Australian sea-lions, Neophoca cinerea, off the west coasst of Western Australia, *Wildlife Research,* **19** (1992), 405–415,

[16] A. M. Hein, C. Hou and J. F. Gillooly, Energetic and biomechanical constraints on animal migration distance, *Ecology letters,* **15** (2012), 104–110.

[17] D. E. Hiebeler and B. R. Morin, The effect of static and dynamic spatially structured disturbances on a locally dispersing population, *Journal of Theoretical Biology,* **246** (2007), 136–144.

[18] R. D. Holt and J. M. Fryxell, Theoretical reflections on the evolution of migration, in *Animal migration: A synthesis* (eds. E. Milner-Gulland, J. M. Fryxell, and A. R. Sinclair), Oxford University Press, New York, NY, ISBN 9780199569007, 17–31.

[19] J. D. Hunter, Matplotlib: A 2d graphics environment, *Computing In Science & Engineering,* **9** (2007), 90–95.

[20] E. Jones, T. Oliphant and P. Peterson, et al., SciPy: Open source scientific tools for Python (2001–), http://www.scipy.org/.

[21] A. Kaitala, V. Kaitala and P. Lundberg, A theory of partial migration, *American Naturalist,* **142** (1993), 59–81.

[22] I. Kovacic and M. J. Brennan, *The Duffing Equation: Nonlinear Oscillators and Their Behaviour*, Wiley, 1 edition, 2011, ISBN 9780470715499.

[23] S. Lenci and G. Rega, Forced harmonic vibration in a Duffing oscillator with negative linear stiffness and linear viscous damping, in *The Duffing Equation: Nonlinear Oscillators and their Behaviour* (eds. I. Kovacic and M. J. Brennan), Wiley, ISBN 9780470715499, (2011), 219–276.

[24] S. Lenhart and J. T. Workman, *Optimal Control Applied to Biological Models*, Chapman & Hall/CRC, 2007, ISBN 9781584886402.

[25] P. Lundberg, Partial bird migration and evolutionarily stable strategies, *Journal of Theoretical Biology,* **125** (1987), 351–360.

[26] J. M. McNamara, A. I. Houston and E. J. Collins, Optimality models in behavioral biology, *SIAM Review,* **43** (2001), 413–466.

[27] B. H. McRae, B. G. Dickson, T. H. Keitt, and V. B. Shah, Using Circuit Theory to Model Connectivity in Ecology, Evolution, and Conservation, *Ecology,* **89** (2008), 2712–2724.

[28] A. Mertz and W. Slough, Graphics with pgf and tikz, PracTeX Journal, **1**, http://www.tug.org/TUGboat/tb28-1/tb88mertz.pdf.

[29] T. Mueller and W. F. Fagan, Search and navigation in dynamic environments–from individual behaviors to population distributions, *Oikos,* **117** (2008), 654–664.

[30] R. Nathan, An emerging movement ecology paradigm, *Proceedings of the National Academy of Sciences,* **105** (2008), 19050–19051.

[31] R. Nathan, W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz and P. E. Smouse, A movement ecology paradigm for unifying organismal movement research, *Proceedings of the National Academy of Sciences,* **105** (2008), 19052–19059.

[32] A. H. Nayfeh and D. T. Mook, *Nonlinear Oscillations*, Wiley, New York, 1995, ISBN 9780471121428.

[33] C. J. Pennycuick, The mechanics of bird migration, *Ibis,* **111** (1969), 525–556.

[34] Python Software Foundation, Python Language Reference, version 2.7 (2010-), http://www.python.org.

[35] T. C. Reluga, J. Medlock and A. P. Galvani, The discounted reproductive number for epidemiology, *Mathematical Biosciences and Engineering,* **6** (2009), 377–393.

[36] D. E. Schindler, R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers and M. S. Webster, Population diversity and the portfolio effect in an exploited species, *Nature,* **465** (2010), 609–612.

[37] A. K. Shaw and S. A. Levin, To breed or not to breed: A model of partial migration, *Oikos,* **120** (2011), 1871–1879.

[38] A. K. Shaw and I. D. Couzin, Migration or residency? the evolution of movement behavior and information usage in seasonal environments, *The American Naturalist,* **181** (2013), 114–124.

[39] A. K. Shaw and S. A. Levin, The evolution of intermittent breeding, *Journal of Mathematical Biology,* **66** (2013), 685–703,

[40] S. C. Stearns, *The Evolution of Life Histories*, Oxford University Presss, Oxford, UK, 1992.

[41] SymPy Development Team, SymPy: Python library for symbolic mathematics, 2013, http://www.sympy.org.

[42] W. Szempli'nska-Stupnicka and K. L. Janicki, Basin boundary bifurcations and boundary crisis in the twin-well Duffing oscillator: Scenarios related to the saddle of the large resonant orbit, *International Journal of Bifurcation and Chaos,* **07** (1997), 129–146.

[43] H. R. Thieme, Spectral bound and reproduction number for infinite-dimensional population structure and time heterogeneity, *SIAM Journal on Applied Mathematics,* **70** (2009), 188–211.

[44] J. M. T. Thompson and H. B. Stewart, *Nonlinear Dynamics and Chaos*, John Wiley and Sons, New York, 2002. ISBN 9780471876847.

[45] J. M. Travis and C. Dytham, Habitat persistence, habitat availability and the evolution of dispersal, *Proceedings of the Royal Society of London. Series B: Biological Sciences,* **266** (1999), 723–728.

[46] P. Wiener and S. Tuljapurkar, Migration in variable environments: Exploring life-history evolution using structured population models, *Journal of Theoretical Biology,* **166** (1994), 75–90.

[47] T. Williams, C. Kelley and many others, Gnuplot 4.4: an interactive plotting program, http://gnuplot.sourceforge.net/ (2010-).

[48] S. Wright, *Evolution and the Genetics of Populations*, Volume 2: Theory of Gene Frequencies, University Of Chicago Press, 1969, ISBN 9780226910390.