On the adaptive use of information in habitat selection

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On the adaptive use of information in habitat selection

by

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B.S., Duke University, 1994

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On the adaptive use of information in habitat selection
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The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline.
Integrating evolution and ecology into mathematical models allows one to study the role of natural selection in ecological interactions. At suitable spatial scales, landscapes are not homogeneous and species interact across spatially variable environments. Thus to better understand organism distributions, it is essential that we know what cues organisms actually use to direct movement. We begin our inquiry by introducing a general model of single-species habitat selection that includes two sources of information, information on fitness and information on resources. In searching for evolutionarily stable strategies of information use, we discover that organisms constrained by perceptual limits may use an arbitrary combination of these two sources of information, but when realistic evolutionary costs are added, the strategy that maximizes fitness is the one that completely ignores information on fitness.

We analyze the model, which is an extension of previous two-patch models with population dynamics, and give sufficient conditions for the existence of an asymptotically stable equilibrium. We prove the global evolutionary stability of several of the information-use strategies, and we show that the addition of costs causes the equilibrium distribution to deviate from the ideal free (or, “equal fitness across patches”) distribution.

Finally, we explore how the evolution of random dispersal of prey, when population dynamics without movement are chaotic, changes with the introduction of a predator. We find that the predator can promote or prevent coexistence of two prey types with different strategies. The outcome depends on the predator mortality rate which has a strong effect on the overall population dynamics of the system.
Dedication

To everyone who helped a friend achieve his dreams.
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I pray that we always remember the gift of human potential for doing good, working hard, and making a difference.
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\[ \text{Parameter values: } r = 3, K_1 = 1000, K_2 = 500, m = 1, b = 0.1, c = 0.03, e_1 = 0.5, e_2 = 0.25. \]
Chapter 1

Introduction

“‘Let them have dominion over the fish of the sea, the birds of the air, and the cattle, and over all the wild animals and all the creatures that crawl on the ground.’” – Genesis 2:26

The world around us is filled with creatures of various shapes and sizes. They inhabit areas so diverse that within the environment one species calls home, other species would perish. The ability of organisms to adapt to their environments is astonishing and powerful. And yet, there are limitations to how far one individual can change itself or its environment in the pursuit of life. Physiological constraints restrict the degree to which organisms can reproduce, gather food, assimilate nutrients, make decisions, move about, and defend themselves. This leads one to ask: in the presence of these limitations, how have so many different types of organisms come to inhabit so many different areas of our world?

1.0.1 Evolutionary dynamics

The answer is evolution. In 1859, Charles Darwin published his book On the Origin of Species in which he expounded on the concept of natural selection, that is, the “preservation of favorable variations and rejection of injurious variations” (Darwin, 2009, pg. 98). These beneficial variations in an organism’s genetic code manifest themselves in an organism’s physiology and may spread throughout a population if these traits offer the bearer higher “fitness.” Here, we adopt the definition of fitness as the relative replication success of a given type. The success of an individual to pass on its genetic material to the next generation is, of course, inextricably linked with the envi-
ronment in which the individual lives, and so, what constitutes a beneficial trait in one environment may be injurious in another. As a trivial example, consider how the effectiveness of an organism’s camouflage depends on the background coloration of the environment in which the organism lives. Individuals with better camouflage will possess a competitive advantage over their peers; that is, they will tend to have higher fitness relative to their peers, all other traits being equal.

From this idea of individual fitness, we can describe how an entire species might evolve. Consider a single species composed of many individuals living in a homogeneous environment. Individual fitness will vary in this environment depending on each individual’s genes. One could assign a “fitness score” to each individual, and those individuals with more favorable heritable traits would earn a higher score relative to the others. The composition of the fitness scores of the species could then be visualized on what Sewall Wright termed a “fitness landscape” (Wright, 1932). In this landscape, the individual gene combinations represent locations, and the topography of the landscape represents the fitness score which is a function of both the gene combinations and the environment. This fitness landscape can have many peaks and valleys. As individuals reproduce, gene combinations and frequencies change, so the location of organisms’ genetic code on this landscape also change. Over time, individuals with higher fitness may cause the entire species to climb up a local fitness gradient as a consequence of natural selection. If the environment is heterogeneous or if fitness is dependent on gene frequency, then the fitness landscape itself may change over time.

One way to model the proportion of individuals with a given trait (or behavior) in a population is as a game. Maynard Smith and Price (1973) took this approach in modeling the evolution of the “limited war” strategy in animal conflicts. They introduced five different strategies that an animal could use against a fellow competitor. Then, they competed the strategies pairwise against each other in a series of computer-simulated contests. The payoffs to each player depended on the strategies being used by each participant in the contest. At the end of the simulations, they computed the average payoffs for every pairwise interaction. Applying the concept of an evolutionarily
stable strategy\(^1\) (hereafter, “ESS,” Maynard Smith and Price, 1973; Maynard Smith, 1982), they showed that the ESS always favored non-lethal aggression unless the opponent chose to escalate the conflict, thereby offering an explanation for non-lethal aggression in animal conflicts. Drawbacks of using this to model evolution are that it does not allow for more than two strategies to compete at a time or the inclusion of population dynamics.

A second game formulation was given by Taylor and Jonker (1978). They introduced a set of differential equations which have come to be called the replicator equations (1.1)

\[
\dot{s}_i = s_i [F(i | s) - F(s | s)].
\] (1.1)

Here, \(s_i\) is the proportion of individuals of a constant population size playing strategy \(i\), \(F(i | s)\) is the fitness of strategy \(i\) playing against the population \(s\), and \(F(s | s)\) is the average fitness of the population. Thus, when strategy \(i\) has higher fitness than the average population fitness, its frequency will increase, whereas when strategy \(i\) has lower fitness than average, its frequency will decrease. Modeled in this form, individuals can compete against an entire population, thus the success of a given strategy depends on the population composition. That is, the success of the strategy is frequency-dependent, since its ultimate payoff will fluctuate with the mean payoff of the population. A drawback of applying (1.1) to model evolution is that the set of possible strategies must be specified at the beginning since if \(s_j = 0\), then \(\dot{s}_j = 0\) for all time (but see Abrams et al., 2007, pg. 512, for incorporating mutations), and population dynamics cannot be introduced (except through a Moran process, e.g., Nowak et al. (2004)).

A third modeling approach, termed “adaptive dynamics,” detailed by Dieckmann and Law (1996), built upon both of the previous ideas and introduced the “canonical equation” of adaptive dynamics (1.2)

\[
\frac{d}{dt}s_i = k_i(s) \cdot \frac{\partial}{\partial s_i}W_i(s', s)|_{s'_i = s_i}.
\] (1.2)

\(^1\) Given two strategies \(U\) and \(V\), \(U\) is an ESS if \(W(U, U) > W(V, U)\), or \(W(U, U) = W(V, U)\) and \(W(U, V) > W(V, V)\) (Maynard Smith, 1982). Here, \(W(U, V)\) is the payoff to an individual playing strategy \(U\) against an opponent playing strategy \(V\).
where $s_i$ is the quantitative trait of species $i$, $k_i(s)$ scales the rate of evolutionary change, and $W_i(s_i', s)$ is the fitness of individuals with trait $s_i'$ in a population with traits $s$. Again, $\frac{ds_i}{dt}$ represents the rate of change of trait $s_i$. (1.2) differs from (1.1) in that fitness differences are represented by a gradient and the rate at which traits change may depend on the composition of all the species’ traits. One can incorporate population dynamics, but this model assumes that evolutionary dynamics occur on a much slower time scale. Therefore, the underlying population dynamics are always assumed to be on a dynamical attractor. Mutations are introduced probabilistically leading to an equation whose dynamics can be simulated (Dieckmann and Law (1996), pg. 589; see also Marrow et al. (1996)).

As might be expected, the outcome of these mutation-selection dynamics depends on the particular system being studied. The evolutionary dynamics can evolve to a fixed point (Geritz et al., 1998), a cycle (Marrow et al., 1992), or a chaotic attractor (Dercole et al., 2010; Dercole and Rinaldi, 2010). Geritz et al. (1997) established how one could combine the evolutionary stability ideas of Maynard Smith and Price (1973) with the convergence stability criteria of Eshel and Motro (1981); Taylor (1989); Christiansen (1991) and the explicit measure of fitness in Metz et al. (1992) to categorize the direction of trait evolution. To introduce their ideas, we need some terminology. Denote the growth rate of a species with trait $y$ (when rare) by $s_x(y) = r(y, E_x)$ where the ecological environment ($E_x$) is determined by a species with trait $x$. Then, define the selection gradient (Marrow et al., 1992) to be

$$D(x) = \frac{\partial s_x(y)}{\partial y} \bigg|_{y=x} . \quad (1.3)$$

When there is an analytic expression for the ecological environment into which the mutant is introduced, one can calculate the selection gradient to determine potential stationary points of evolution called evolutionarily singular strategies, denoted $x^*$ (Geritz et al., 1998). These are critical points of $s_x(y)$, thus $D(x^*) = \frac{\partial s_{x^*}(y)}{\partial y} \bigg|_{y=x^*} = 0$. These singular strategies are defined to be
evolutionarily stable if
\[ \frac{\partial^2 s_{x^*}(y)}{\partial y^2} \bigg|_{y=x^*} < 0, \] (Maynard Smith, 1982; Geritz et al., 1998) (1.4)

which ensures that at \( x^* \), fitness is maximized. The definition of an ESS implies that once the ESS is established, it cannot be supplanted by any other nearby strategy. However, there are no requirements that an evolutionary path lead to an ESS. Thus, to ensure that the ESS can become established, one considers the convergence stability of a strategy (Eshel and Motro, 1981; Taylor, 1989; Christiansen, 1991). A one-dimensional strategy, \( x^* \), is \textit{convergence stable} if whenever there exist two strategies \( x_1 \) and \( x_2 \) such that \( x_1 < x_2 < x^* \) or \( x^* < x_2 < x_1 \), then a species with strategy \( x_2 \) can always increase when rare when competing against a species with strategy \( x_1 \) whereas a species with strategy \( x_1 \) can never increase when rare when competing against a species with strategy \( x_2 \) (Taylor, 1989; Christiansen, 1991). A sufficient condition for a strategy to be convergence stable is
\[
\frac{\partial^2 s_{x^*}(y)}{\partial x^2} > \frac{\partial^2 s_{x^*}(y)}{\partial y^2} \quad (1.5a)
\]

which is equivalent to
\[
\frac{\partial^2 s_{x^*}(y)}{\partial x \partial y} + \frac{\partial^2 s_{x^*}(y)}{\partial y^2} < 0 \quad (1.5b)
\]

where the derivatives are evaluated at \( x^* \) (Geritz et al., 1997, 1998). Something very interesting happens if a strategy is convergence stable, but not an ESS. In this case, \( \frac{\partial^2 s_{x^*}(y)}{\partial x^2} + \frac{\partial^2 s_{x^*}(y)}{\partial y^2} > 0 \), and evolutionary branching can occur (Geritz et al., 1998). Thus, a coalition with two different strategies may emerge. This has been posed as a potential mechanism of sympatric speciation.

We have neglected to mention how the evolution of traits can affect the underlying ecology. We do so briefly here. In cases where the ecological system is far from a bifurcation point (in the parameter(s) subject to evolution), then introducing a mutant whose evolutionary parameters are close to those of the resident will not change the ecological attractor of the combined system (Geritz et al., 2002). In Lotka-Volterra systems, coexistence of the resident and mutant species is not possible (Dieckmann, 1994). Whether the mutant and resident coexist for general systems is
an open question. In most cases, researchers rely on simulations of evolutionary systems to gain insight on the final species composition.

1.0.2 Optimal habitat selection

The vast majority of evolutionary studies have focused on multi-species systems that evolve in one spatial location (Marrow et al., 1992, 1996; Dieckmann and Law, 1996; Cortez and Ellner, 2010; Mougi and Iwasa, 2010; Kisdi and Geritz, 2010; Mougi and Iwasa, 2011). However, one could argue that we must include this dimension in our explorations of the evolution of traits since ecology is inherently spatial. That is, evolution can have an impact on the rate at which organisms move through their environment either to forage, avoid predators, choose habitat, or for any combination of these activities. There are a number of studies on the evolution of dispersal which we will introduce in later sections, but because of the importance of habitat selection and its relevance to this work, we will focus here on the development of habitat selection models subject to evolution.

Two early influential papers on habitat selection modeled the question in the following way (Charnov, 1976; Rosenzweig, 1981). Consider a patchy environment where good foraging patches exist within an otherwise unprofitable landscape. A forager will consume resources locally thereby depressing the abundance of food in that patch. At what point in time should the consumer move to another patch? The answer is that it should abandon the current patch when the marginal rate of return in that patch falls below the average rate of return for all of the patches (Charnov, 1976). Rosenzweig (1981) extended the analysis to show that habitat selection could promote the coexistence of two foragers if both are generalists until such time that their abundances drop too low at which point they temporarily become specialists in their preferred type of patch.

Brown (1990) revisited this question using evolutionary game theory (Vincent and Brown, 2005), a formulation similar to the “adaptive dynamics” framework of Dieckmann and Law (1996). The pure foraging strategies he considered were (1) specialize in single patch, or (2) forage in both patches (be a generalist), and the evolutionary parameter was the proportion of time spent playing each strategy. He found that different strategies were selected for depending on the relative
disparity of the qualities of the patches and on whether movement was costly.

Křivan et al. (2008) reviewed how game theory has been used recently to model habitat selection. The standard approach has been to solve for the proportion of time an optimally acting individual should spend playing one pure strategy or another. This approach has yielded substantial insight on, for example, the two-patch dynamics of optimally moving predators and prey (Křivan, 1997), habitat selection of two competing species (Křivan and Sirot, 2002), animal behavior coupled with population dynamics (Cressman et al., 2004), and optimal migration (Cressman and Křivan, 2006).

A potential shortcoming of this modeling approach is that although the optimal strategy describes the proportion of time an individual should devote to one or another strategy, it does not describe how an organism might move between patches. In other words, it cannot answer the question: what inputs might “drive” movement? Abrams et al. (2007) reviewed several two-patch models of optimal habitat selection that incorporated the population dynamics of multiple species and diffusive and adaptive movement at multiple trophic levels (they considered “adaptive” to mean “movement to areas of higher fitness”). They observed that there can be important feedback between population dynamics and adaptive (optimal) movement. Namely, adaptive movement and the behavioral dynamics of adaptation can cause population oscillations, and population oscillations generally affect which movement strategies are optimal (Abrams, 2007). Whether these oscillations are reinforcing or damping may very well depend on the types of information sources used in assembling an adaptive strategy. Categorizing the dynamical interplay between population dynamics and the adaptive use of various information sources to guide movements is an open problem.

Although there is some evidence that organisms might use fitness as a source of information to guide movement (Bowler and Benton, 2005), and several previous studies have assumed organisms have access to this information (e.g., Křivan, 1997; Abrams, 2000; Armsworth and Roughgarden, 2005; Abrams, 2007), it has been shown that the use of other sources of information may lead to movement behaviors that are just as adaptive (Flaxman and Lou, 2009; Morris, 2011; Galanthay and Flaxman, 2012). To explore this idea, we will consider in chapters 2 and 3 a general habitat
selection model of the form

\[
\begin{align*}
\dot{x}_1 &= x_1 f_1(x_1) - \epsilon_1(x_1, x_2; \alpha) + (1 - k)\epsilon_2(x_1, x_2; \alpha) \\
\dot{x}_2 &= x_2 f_2(x_2) + (1 - k)\epsilon_1(x_1, x_2; \alpha) - \epsilon_2(x_1, x_2; \alpha)
\end{align*}
\tag{1.6a}
\tag{1.6b}
\]

where \(x_i\) and \(f_i\) represent a consumer species and its per capita growth rate in patch \(i\), respectively, and \(k\) represents the fitness cost of moving between patches. \(\epsilon_i\) controls movement between patches and is a function of \(x_1, x_2\) and several parameters. In this form, \(\epsilon_i\) controls both the proportion of information sources upon which an organism might base its movement rates and also the relative rate at which it acts upon those information sources. Since the \(x_i\) change over time, the per capita movement rates between patches may change over time. Through the analysis of systems like (1.6), we can use dynamical systems theory to discover optimal information-use strategies to guide movement, thereby gaining a deeper understanding of the effects of evolution on habitat selection.
Chapter 2

Adaptive information-use strategies in single-species habitat selection

2.1 Introduction

Ecologists have long sought to explain spatial distributions of organisms. At small spatial scales, Fretwell and Lucas’s (1969) ideal free distribution model has been extended and widely applied to explain and predict spatial relationships between resources and the organisms that consume them (see also reviews by Tregenza 1995 and Krivan et al. 2008). In general terms, an ideal free distribution (hereafter, “IFD”) is a spatial distribution of consumers at which no individual consumer can improve its fitness by moving to a different location (Fretwell and Lucas, 1969). Models considering habitat selection and IFDs generally fall into one of two categories (Kacelnik et al., 1992): (1) “equilibrium” models that predict the distribution that should be achieved by optimally-behaving consumers, and (2) “dynamic” models that ask whether a given habitat selection strategy or specific movement dynamics will lead to any equilibrium (IFD or otherwise; see also review by Flaxman and Lou 2009).

Equilibrium models have been very useful in illuminating patterns that might exist when organisms can approximate optimal behavior, and such models have found consistent empirical support, though exceptions can certainly be found (reviewed by Tregenza, 1995; Cressman and Krivan, 2006; Krivan et al., 2008). However, equilibrium models’ explicit lack of any notion of actual behaviors or dynamics leaves a gap in understanding the mechanisms that produce observed patterns in nature (Turchin, 1998). The need to explore the mechanistic basis of movement and habitat selection (and other behaviors and ecological patterns as well) has long been recognized...
(Lima, 2002; Sih, 2005; Nathan, 2008; Nathan et al., 2008; McNamara and Houston, 2009), and, accordingly, many dynamic, process-based models of movement and habitat selection have been developed over the years.

Models studying movement dynamics and the IFD have been recently reviewed by Cressman and Krivan (2006), Abrams et al. (2007), Krivan et al. (2008), and Abrams (2010). A feature of most of these models is that movement is instantaneous and free of cost (Abrams et al., 2007). Under these assumptions, Cressman and Krivan (2006) showed that in a single species habitat-selection game, the population will be distributed at the IFD when individuals use dispersal rules that do not allow organisms to move to patches with a lower payoff. Furthermore, they showed that strategies leading to the IFD are evolutionarily stable strategies (hereafter, “ESSs”) (Maynard Smith, 1982; Cressman and Krivan, 2006). The concept of the IFD in multi-species models is more complex. For example, Krivan et al. (2008) demonstrated that the stability of the multi-species IFD depends on the particular dispersal rules used. This finding should motivate the study of general movement rules that can lead to stable multi-species IFDs (Flaxman and Lou, 2009; Flaxman et al., 2011). Here, we restrict our attention to general rules that are adaptive for a single species (a single variant) by itself or in competition with a second species (or alternative variant); our future work will extend these studies to more general multi-species contexts.

It is well known that in temporally constant but spatially heterogeneous environments, in the absence of kin selection or asymmetric competition, that unconditional dispersal will be selected against (Hastings, 1983; Holt, 1985; Dockery et al., 1998). However, when organisms are able to condition their movement on habitat type such that net movement is zero at equilibrium, i.e., “balanced dispersal” (McPeek and Holt, 1992), selection will be for conditional dispersal (McPeek and Holt, 1992; Padron and Trevisan, 2006; Kirkland et al., 2006; Cantrell et al., 2007a). In discrete space, balanced dispersal strategies are evolutionarily stable (Kirkland et al., 2006; Cressman and Krivan, 2006, 2010) and can invade other conditional strategies; however, since balanced dispersal strategies are neutrally stable (McPeek and Holt, 1992; Cantrell et al., 2007b), selection is not sufficient for one balanced dispersal strategy to exclude another. In sum, balanced strategies, and
potentially other dispersal strategies that allow populations to match the quality of the environment, can be evolutionarily stable (Cantrell et al., 2010; Averill et al., 2012).

The evolutionary stability of conditional dispersal strategies has been studied with discrete patch models and also with continuous space models. Continuous space models have generally taken the form of reaction-diffusion-advection equations or some variant of these (see, e.g., Okubo, 1980; Okubo and Levin, 2001). Common features of these models are density-dependent growth, a diffusion rate greater than or equal to zero, and, when advection is considered, movement up one or several gradients. Dockery et al. (1998) confirmed, with a reaction-diffusion model, that slower diffusion rates are adaptive. Belgacem and Cosner (1995) showed, using a diffusion-advection model, that in some environments, conditional movement up a resource gradient can be adaptive. More recent work has incorporated environmental temporal dynamics (Hutson et al., 2001), refined the conditions under which advection along a resource gradient is adaptive (Cosner and Lou, 2003; Cantrell et al., 2006, 2007b; Chen et al., 2008; Cantrell et al., 2010; Averill et al., 2012), and considered advection along gradients other than the resource gradient (Flaxman and Lou, 2009). For a recent review, see Lou (2008).

Most theoretical studies of single-species movement dynamics (and the evolutionary stability of movement strategies) where movement rules are a function of conditions of the environment have not included movement based directly on an organism’s fitness (but see Cressman and Křivan, 2006; Cantrell et al., 2008; Křivan, 2008); rather, movement rules based on the heterogeneity of the resource are more common. Intuitively, one might assume that if information based upon fitness is available, organisms should use it. Indeed, it would seem almost tautological that movement conditioned upon fitness information should maximize fitness. Cantrell et al. (2008) showed that when organisms move diffusively and also advect up a fitness gradient, the IFD (sensu Cosner, 2005) could be approximated only when the rate of advection approached infinity or the rate of diffusion approached zero (see Cressman and Křivan, 2006, for a similar result in discrete space). Thus, it seems unlikely, in the presence of any diffusive movement, that there would exist an ESS that relies solely upon information on fitness.
From the brief overview we have given of the evolutionary stability of dispersal strategies, it would seem reasonable that when organisms have limited information and make occasional errors (which can be approximated by a diffusion term), there might be two different strategies of local information use that would lead to fitness maximization and ideal free distributions, namely, optimally moving organisms either (1) use local fitness information and move infinitely fast or (2) use local resource information to create a balanced dispersal strategy. However, it is not clear which of these two strategies might be more adaptive. Nor has it been proven that this list of strategies is exhaustive. It thus bears investigating: What general information-use strategies for movement will be favored by natural selection?

We begin with a simple movement model that incorporates both unconditional and conditional movement behaviors to discover an optimal movement strategy, that is, a strategy that maximizes fitness. For clarity, in our usage “unconditional movements” are movements that are not influenced in any way by an organism’s state or that of its environment. There are many reasons why such movements may occur in real organisms (McPeek and Holt, 1992; Hugie and Grand, 1998), and as such, we impose some rate of diffusive movement as a constraint on the organisms. This constraint is imposed as a simple way of representing errors in assessment of current conditions, perceptual limitations on assessment, or movement for reasons other than consuming resources (e.g., fitness-related factors that we do not explicitly consider). In contrast, “conditional movements” are those that are made in response to available information. For our purposes, a single “movement” is a change from one discrete patch of habitat to another, and we assume that the spatial scale of these movements is such that an individual organism can make many movements in its lifetime.

In our model, we allow organisms the flexibility to prioritize their use of information on fitness or habitat. While we recognize that it may not be realistic for organisms to have information on their fitness per se, many previously published works (e.g., Abrams, 2000, 2007; Armsworth and Roughgarden, 2005; Cressman and Křivan, 2006; Abrams et al., 2007; Abrams and Ruokolainen, 2011) assume it to be possible (and adaptive), so we allow organisms this capability. Since we do
not specify a precise information-use strategy, we do not need to assume a priori that a particular behavior is adaptive. Instead, we allow natural selection, via the framework of invasion analysis, to form an organism’s best use of information in generating an optimal, adaptive movement strategy (Metz et al., 1992; Meszéna et al., 2005, and references therein). To accomplish this, we follow the approach of many of the studies mentioned above, to wit, we begin with two variants of a single species that differ only in their strategy of information use and ask if one of these (a mutant) can invade the other (a resident) and increase in abundance.

Our goal is to explore how organisms should use available information in guiding conditional movements by studying the evolutionary stability of various information-use strategies. In models where movement is conditioned on time-dependent quantities and fitness is not an explicit function of strategies, analytical results are often impossible to find, and investigators tend to rely on numerical results to make conclusions. Our model incorporates behaviors and environmental interactions but is simple enough also to allow us to find an analytical expression for an evolutionarily stable strategy. This strategy is an ideal combination of movement conditioned on fitness and habitat information that, in the presence of random movement, achieves the IFD and is therefore an evolutionarily stable movement strategy in the sense of Cressman and Krivan (2010). We confirm through numerical simulations, using ideas from adaptive dynamics (Metz et al., 1992; Diekmann, 2004; Kisdi and Geritz, 2010, and references therein), that this strategy that leads to the IFD is evolutionarily stable and also convergence stable, meaning that the ESS is also an evolutionary attractor. In addition, we show that our simple model synthesizes many previous authors’ theoretical results obtained from the use of a wide variety of models. Then, we consider how costs might affect the evolutionary stability of our strategies. Finally, we discuss implications of the optimal strategy and conclude that although fitness-based movement can be part of an evolutionarily stable movement strategy, when realistic movement costs are considered, fitness-based movement is not, in general, adaptive.
2.2 Methods

2.2.1 The model

We consider a single species able to move within a discrete two-patch environment. We allow organisms to move, initially without cost, from one patch to another via both undirected (discrete diffusion) and directed (fitness-dependent and habitat-dependent) movement. The rate of conditional movement can depend upon the magnitudes of both the relative fitness differential between patches (Armsworth and Roughgarden, 2005; Abrams, 2007) and the relative differences in habitat quality between patches (McPeek and Holt, 1992).

In our consumer-resource model, we assume that the intrinsic quality of patches remains constant over time. The variables used are summarized and defined in table 2.1. For a single population, the dynamical equations are:

\[
\dot{N}_1 = f(N_1; K_1) \cdot N_1 - d(N_1 - N_2) + m[\tau \cdot \max(0, \tilde{N}) + (1 - \tau) \cdot \max(0, \tilde{K})]N_2 - m[\tau \cdot \max(0, -\tilde{N}) + (1 - \tau) \cdot \max(0, -\tilde{K})]N_1
\]

\[
\dot{N}_2 = f(N_2; K_2) \cdot N_2 + d(N_1 - N_2) - m[\tau \cdot \max(0, \tilde{N}) + (1 - \tau) \cdot \max(0, \tilde{K})]N_2 + m[\tau \cdot \max(0, -\tilde{N}) + (1 - \tau) \cdot \max(0, -\tilde{K})]N_1
\]

with

\[
\tilde{N} = \left( f(N_1; K_1) - f(N_2; K_2) \right) / \left( r \left( \frac{N_1}{K_1} + \frac{N_2}{K_2} \right) \right) = \frac{N_2/K_2 - N_1/K_1}{N_2/K_2 + N_1/K_1}
\]

and

\[
\tilde{K} = \frac{K_1 - K_2}{K_1 + K_2},
\]

where \( N_i \) is the abundance of organisms in patch \( i \) (\( i = 1, 2 \)), the rate of change in this abundance is denoted \( \dot{N}_i \) (\( \equiv \frac{dN_i}{dt} \)), and the population dynamics are governed by the logistic equation, \( f(N_i; K_i) = r(1 - \frac{N_i}{K_i}) \). Competition in the model thus arises from density-dependent growth. The growth parameters influencing fitness in each patch are defined as follows: \( r \) is the consumer’s intrinsic growth rate, and \( K_i \) is the carrying capacity of patch \( i \). Throughout this chapter, we will assume
that patch 1 is the better patch, i.e., $K_1 > K_2$. For clarification, when we refer to the “fitness in a patch,” we mean the instantaneous growth rate, that is, the per capita growth function, $f(N_i; K_i)$. An organism’s fitness is its relative replication rate. This quantity will depend on its information-use strategy, since this strategy affects the organism’s location and thus influences the organism’s ability to capitalize on the instantaneous growth rate of each patch. Note that at an IFD, patch suitabilities must be equal. Therefore, in our model, organisms are at an IFD whenever $f(N_1; K_1) = f(N_2; K_2)$.

Movements are governed by the unconditional movement rate parameter, $d$, and by the conditional movement strategy, which is defined by the two variables $m \geq 0$ and $\tau \in [0, 1]$. A strategy is thus a two-element vector, $(m, \tau)$. In biological terms, $m$ represents the strength of response (expressed as a rate) to differences between patches, and $\tau$ represents information use, explained more below.

Information on differences between patches is expressed as $\tilde{N}$ (fitness information) and $\tilde{K}$ (habitat information). $\tilde{N}$ is the per capita growth rate difference between patch 1 and patch 2, normalized so that $-1 \leq \tilde{N} \leq 1$. A positive value of $\tilde{N}$ indicates that patch 1 has a higher per capita growth rate than patch 2 whereas a negative value of $\tilde{N}$ indicates that patch 2 has a higher per capita growth rate than patch 1. Since $\tilde{N}$ is based upon the realized per capita rates of increase in each patch, it is a direct measure of the fitness difference between the two patches for a given distribution $\{N_1, N_2\}$ of consumers. $\tilde{K}$ is the carrying capacity difference between patches, normalized so that $-1 \leq \tilde{K} \leq 1$. Given our assumption above that $K_1 > K_2$, we will have $\tilde{K} > 0$ (see definition of $\tilde{K}$, above).

The relative priority assigned to available information is governed by $\tau$, which is defined as the proportion of fitness-based information used in guiding conditional movement, i.e., a value of $\tau = 1$ corresponds to exclusive use of fitness information whereas a value of $\tau = 0$ corresponds to no use of fitness information. By placing no constraints on $m$ (only that it is non-negative and finite), we allow organisms to act upon one or both sources of information to any arbitrary degree. Indeed, one can view the realized movement rate in response to a given $\tilde{N}$ as $m\tau$ and the realized
movement rate in response to $\tilde{K}$ as $m(1 - \tau)$. Since $\tau$ and $m$ can be changed independently of one another, limiting $\tau$ to $[0, 1]$ in no way restricts the set of possible information-use strategies.

We note that $d$ is assumed to be a fixed constant that we do not allow to evolve. This term defines a baseline level of suboptimal movement (or “non-IFD movement” sensu Hugie and Grand (1998)). Reasons for non-IFD movement may include simple errors or movement for reasons other than obtaining resources (Milinski, 1988; Hugie and Grand, 1998).

In order to consider the evolutionary and convergence stability of a strategy, we introduce a mutant ($M$) at a small frequency into a resident population ($N$). The mutant is identical to the resident except for its information-use strategy. The dynamics of this are defined by:

$$\dot{N}_1 = g(N_1, M_1; K_1) \cdot N_1 - d(N_1 - N_2) + m_R[\tau_R \cdot \max(0, \tilde{N}) + (1 - \tau_R) \cdot \tilde{K}]N_2$$

$$- m_R[\tau_R \cdot \max(0, -\tilde{N})]N_1$$

$$\dot{N}_2 = g(N_2, M_2; K_2) \cdot N_2 + d(N_1 - N_2) - m_R[\tau_R \cdot \max(0, \tilde{N}) + (1 - \tau_R) \cdot \tilde{K}]N_2$$

$$+ m_R[\tau_R \cdot \max(0, -\tilde{N})]N_1$$

$$\dot{M}_1 = g(M_1, N_1; K_1) \cdot M_1 - d(M_1 - M_2) + m_M[\tau_M \cdot \max(0, \tilde{N}) + (1 - \tau_M) \cdot \tilde{K}]M_2$$

$$- m_M[\tau_M \cdot \max(0, -\tilde{N})]M_1$$

$$\dot{M}_2 = g(M_2, N_2; K_2) \cdot M_2 + d(M_1 - M_2) - m_M[\tau_M \cdot \max(0, \tilde{N}) + (1 - \tau_M) \cdot \tilde{K}]M_2$$

$$+ m_M[\tau_M \cdot \max(0, -\tilde{N})]M_1$$

where now

$$\tilde{N} = \left( g(N_1, M_1; K_1) - g(N_2, M_2; K_2) \right) / \left( r \left( \frac{N_1 + M_1}{K_1} + \frac{N_2 + M_2}{K_2} \right) \right),$$
Table 2.1: Parameter definitions and values

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Definitions</th>
<th>Values used in simulations</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r$</td>
<td>Intrinsic growth rate</td>
<td>$r = 1$</td>
</tr>
<tr>
<td>$K_i$</td>
<td>Carrying capacity of patch $i$</td>
<td>$K_1 = 20, K_2 = 10$</td>
</tr>
<tr>
<td>$d$</td>
<td>Random movement rate</td>
<td>$d = 0.1$</td>
</tr>
<tr>
<td>$m_R (m_M)$</td>
<td>Strength of response of resident (mutant), expressed as a rate, to assessed differences between patches</td>
<td>varies</td>
</tr>
<tr>
<td>$\tau_R (\tau_M)$</td>
<td>Proportion of fitness information used to guide conditional movements of the resident (mutant)</td>
<td>varies</td>
</tr>
<tr>
<td>$k$</td>
<td>Movement cost parameter</td>
<td>varies</td>
</tr>
</tbody>
</table>

$\tilde{K}$ is defined as before (and $\tilde{K} > 0$), and subscript $i (i = 1, 2)$ continues to denote patch number $i$.

Since the resident and mutant consume resources in the same patches, the fitness function becomes:

$$g(N_i, M_i; K_i) = g(M_i, N_i; K_i) = r(1 - \frac{N_i + M_i}{K_i}) = f(N_i + M_i; K_i).$$

For the majority of our work, we vary $m$ and $\tau$ and leave the other parameters constant (table 2.1). We will denote the resident’s strategy as the pair of values $(m_R, \tau_R)$ and the mutant’s strategy as the pair of values $(m_M, \tau_M)$. We note that the analytical solutions we derive are independent of parameter values used. For results based upon numerical analyses, examples shown here were obtained with the parameter values in table 2.1. Results with alternative parameter values are available upon request.

### 2.2.2 Calculating the evolutionarily stable strategy candidate

For our single-species model, the equilibrium population will be distributed at the IFD when the populations in each patch are simultaneously at their carrying capacities (Parker and Sutherland, 1986). Cressman et al. (2004) show that the optimal strategy in the single-species habitat game must lead to full carrying capacity in all patches. This is an IFD as defined above since, at this distribution, no organism can improve its fitness by moving to the other patch. Thus, movement that leads to the IFD resembles, at an equilibrium, no movement at all. Cressman and Krivan (2006) showed that in the absence of population dynamics, a single-species dispersal strategy that
leads to an IFD is an ESS. In other words, if our model did not include population dynamics, we could identify an evolutionarily stable strategy simply by finding a strategy that leads to an IFD. This motivates us to begin searching for an “ESS candidate” (Vincent and Brown, 2005) for our model by identifying the movement strategy that would lead to the IFD where both patches are at carrying capacity. Then, applying the definition of ESS (as described below, in “Results”) and invasibility analysis, we test if this candidate strategy is an ESS.

To solve for this ESS candidate, first note that if the species is distributed at the IFD where abundances in both patches are at carrying capacity at equilibrium, then the following must hold: \( N_1 = K_1, N_2 = K_2, \hat{N}_1 = \hat{N}_2 = 0 \). Applying this to equation (2.1a) gives \( 0 = -d(K_1 - K_2) + m(1 - \tau)(\tilde{K})K_2 \). After rearranging and simplifying, the ESS candidate, denoted by \((m^*, \tau^*)\), is defined by pairs of values of \( m \) and \( \tau \) that satisfy

\[
m^* = C \cdot \frac{d}{1 - \tau^*},
\]

(2.3a)

which is equivalent to

\[
\tau^* = 1 - C \cdot \frac{d}{m^*}
\]

(2.3b)

where \( C = (1 + \frac{K_1}{K_2}) \). At different times in this paper, we will find it convenient to refer to one formulation or the other. Also note that the same ESS candidate would be derived from equation (2.1b). For notational convenience, when the resident’s strategy parameters satisfy (2.3a), we will write \((m^*_R, \tau^*_R)\) instead of \((m_R, \tau_R) = (m^*, \tau^*)\) (similarly for the mutant).

**Remark:** For fixed \( d, K_1 \), and \( K_2 \), there exists a continuum of \( m \) and \( \tau \) values that satisfies equations (2.3). Rather than refer to a particular movement strategy as a member of the ESS candidate set, we will, for convenience, refer to any pair of \( m \) and \( \tau \) values that satisfies equations (2.3) as an ESS candidate.

### 2.2.3 Assessing the stability of the candidate strategy

We assessed the evolutionary stability of the candidate strategy through numerically simulated invasion analysis. To wit, we conducted two types of simulations, the first to show that the
ESS candidate could not be invaded by any other strategy and the second to show that the ESS candidate could invade any other strategy. We also assessed the convergence stability of the ESS candidate using a variation of the first type of simulation (described below).

In the first type of simulation, we allowed a resident population playing the ESS candidate to reach equilibrium (where \( N_1 = K_1 = 20, N_2 = K_2 = 10 \)). Then, we introduced a mutant population \((M)\) into both patches at low levels and continued the simulation. Specifically, in results shown here, mutants were introduced to both patches at initial abundances \( M_1 = M_2 = 1 \). Results were qualitatively the same regardless of initial mutant abundances (whether this common or very rare); we show results for these initial values for the visual clarity they offer in our figures. The fact that our results hold for a wide range of mutant invasion abundances suggests that our conclusions about evolutionary stability are highly robust. For the mutant population, we explored all possible \((m_M, \tau_M)\) combinations with values of \( m_M \) ranging uniformly in increments of 0.05 from 0 to 4 and values of \( \tau_M \) ranging uniformly in increments of 0.01 from 0 to 0.90 (wider ranges of \( m \) and \( \tau \) were considered but did not change the conclusions given here). In each instance of the simulation, we considered only pairwise contests between the mutant and the resident, i.e., only one mutant strategy at a time was competing against the resident’s ESS candidate strategy. This is consistent with the assumption in adaptive dynamics, which we adopt to make our analysis tractable, that the rate of mutations occurs on a time scale slower than the ecological processes. Thus, we do not consider here potential competition among more than two participants. Some of the \((m_M, \tau_M)\) pairs satisfied equations (2.3). Once results were obtained (integration times mentioned below), we repeated the simulations for various other resident \((m^*_R, \tau^*_R)\) pairs. This type of simulation allowed us to observe the ability of the ESS candidate to resist invasion. To assess convergence stability, we relied upon the multi-trait linear stability criteria derived by Abrams et al. (1993), explained in “Results” below. We approximated derivatives of the final mutant population abundance with respect to various combinations of the strategy parameters (e.g., \( m_R, \tau_R, m_M, \tau_M \)) and evaluated these derivatives at \( m_R = m_M = m^*, \tau_R = \tau_M = \tau^* \). We allowed \( \tau^* \) to vary between 0.10 and 0.90 by 0.10. The corresponding value of \( m^* \) was calculated using (2.3a), and the other parameters
were fixed as per table 2.1. Finally, we calculated estimates of the requisite second derivatives and mixed partial derivatives by standard central differences (Burden and Faires, 2005) using a step size of $10^{-4}$.

In the second type of simulation, we allowed a resident population with an arbitrary strategy (not necessarily an ESS candidate) to reach equilibrium. Then, we introduced a rare mutant (again, $M_1 = M_2 = 1$) playing an ESS candidate and continued the simulation. We chose resident values of $m_R$ ranging uniformly in increments of 0.05 from 0 to 4 and $\tau_R$ ranging uniformly in increments of 0.01 from 0 to 0.90. As above, we considered only pairwise contests between the mutant and the resident. Once the results were recorded, we repeated this process for several different $(m^*_M, \tau^*_M)$ ESS candidates. This type of simulation allowed us to observe the ability of the ESS candidate to invade.

We conducted all of the simulations mentioned above using a backward differentiation formula (BDF) scheme in MATLAB (ode15s, with an error tolerance of $10^{-8}$). This numerical integrator, ode15s, works well when solving a system of differential equations like ours where the Jacobian matrix is ill-conditioned (i.e., the largest and smallest eigenvalues differ by orders of magnitude, also known as “stiff” systems). In our system, this occurs when the resident and mutant strategies are similar. Once resident populations reached equilibrium, we continued simulations of the resident-mutant system for an integration time of $1.5 \times 10^6$, except when assessing convergence stability. In that case, we were comparing two very similar strategies. Since convergence can be slow when similar strategies are competed, and for higher accuracy of the derivative calculations, we increased the integration time to $4.5 \times 10^6$ and the error tolerance to $10^{-12}$.

### 2.2.4 Adding movement costs

We considered two different realistic types of costs that might affect movement. First, we examined the effects of costs due to moving through unprofitable areas between patches (Morris, 1992) where predation risks or other migration costs could reduce survival. Second, we examined the effects of costs imposed by developing and maintaining the sensory machinery necessary for
assessing differences between patches.

IFD theory, as defined by Fretwell and Lucas (1969), assumes that movement between habitats is cost-free. It may be more realistic, however, to assume that patches may not be so close as to allow cost-free travel between them (Bernstein et al., 1991). We incorporated the first type of cost — a cost of travel through unprofitable areas — into our model by multiplying the positive immigration terms by a coefficient of survival. For example, to account for this cost in equation (2.1a), we multiplied the expression \( dN_2 + m[\tau \cdot \max(0, \tilde{N}) + (1 - \tau) \cdot \max(0, \tilde{K})]N_2 \) by \((1 - k)\), where \(k\) is a fixed cost that varies between 0 and 1 (see equations (B.11a) and (B.11b) in appendix B for the reformulated equations).

We explored costs of the development and maintenance of sensory machinery by introducing the terms \(-mkN_1\) and \(-mkN_2\) respectively to equations (2.1a) and (2.1b) (see equations (B.13a) and (B.13b) in appendix B for the reformulated equations). The rationale here is that larger values of \(m\) indicate a greater sensitivity to differences in quality between patches. As such, this type of cost assumes that to have a larger value of \(m\), an organism must invest more in the development and maintenance of the sensory organ(s) that it uses to gather information.

In the absence of travel costs, there are two notions of the IFD. The first is a spatial distribution of consumers where no individual can improve its fitness by moving between patches, and the second is a distribution at which fitness is equal between patches. When travel costs exist, these two notions are not equivalent. In the first case, there will be no net movement at an IFD even if fitness between patches is not necessarily equal. That is to say, at an IFD, there may exist a fitness difference between patches less than or equal to the fitness cost one would pay to travel between patches (Rosenzweig, 1981; Morris, 1987; DeAngelis et al., 2011). Several works on the effects of travel costs on movement between patches (Rosenzweig, 1974; Charnov, 1976; Rosenzweig, 1981) have relied on this definition of the IFD (Morris, 1987; Kennedy and Gray, 1993; Astrom, 1994; Kirkland et al., 2006; Matsumura et al., 2010; DeAngelis et al., 2011). This differs from the second notion of “equal fitness between patches” where, although organisms will certainly stop once the IFD is reached, they may in fact stop before the IFD is reached if travel costs are sufficiently high.
However, in order to better compare and contrast the effects of different costs on the ESS candidate, we will continue to use Fretwell and Lucas’ original IFD definition (i.e., \( f(N_1; K_1) = f(N_2; K_2) \)) (Fretwell and Lucas, 1969).

2.3 Results

We describe here some characteristics of the ESS candidate, then we explore the evolutionary and convergence stability of the ESS candidate. This is done first without costs and then with costs.

2.3.1 Properties of the ESS candidate solution

Inspection of equation (2.3b) shows that for any \( d > 0 \), we have \( \tau^* < 1 \); that is, \( \tau^* \) cannot equal 1 unless \( m^* = \infty \). To be biologically realistic, \( m \) must take finite values only, and thus the solution for \( \tau^* \) indicates that, in the presence of some diffusive movement, purely fitness-based movement (\( \tau = 1 \)) cannot lead to fitness maximization or an IFD. By contrast, from inspection of equation (2.3a), we see that for \( \tau^* = 0 \), \( m^* \) is defined, finite, and greater than zero. That is, conditional movement based exclusively on habitat characteristics can lead to an ideal free distribution. For any \( 0 < \tau^* < 1 \), we again find finite values of \( m^* \), and thus the use of a mix of fitness and habitat information can also lead to an IFD.

2.3.2 Evolutionary stability of the ESS candidate

An ESS is an uninvadable strategy such that an individual playing any other strategy against this strategy will have reduced fitness (Maynard Smith, 1982). It is standard practice in evaluating an ESS candidate to analyze equations for the payoff (fitness) to an individual playing the ESS candidate (Maynard Smith, 1982; Vincent and Brown, 2005). Such an approach is possible, for example, when the habitat selection strategy is explicitly expressed as a “residence strategy,” that is, the proportion of time that the organism spends in each patch (e.g., Cressman et al., 2004; Cressman and Garay, 2006; Cressman and Krivan, 2010). In that case, the evolutionary stability of a strategy is often analyzed using standard game-theoretic approaches based upon differentiation
of a fitness function. With our approach, we cannot explicitly write the fitness of an individual playing a given strategy (or, in short, the fitness of a strategy) since the proportion of time an organism spends in each patch depends on the changing population in each patch. Indeed, this is a consequence of one of the important strengths of our model: rather than assuming the relationship between a strategy and its fitness, the fitness of a strategy emerges as a result (a mutant’s fitness is determined by whether the mutant increases or decreases in abundance relative to the resident).

Since there does not exist a closed-form expression for the fitness of a strategy, we cannot use the standard game-theoretic approaches mentioned above. In lieu of this, we rely on the results of numerical simulations of the model to confirm that the ESS candidate is an ESS and also convergence stable. Sufficient conditions for a strategy to be an ESS is for the strategy to be a strict Nash equilibrium, that is to say, a strategy that is the best response to itself.

To show that \((m^*, \tau^*)\) is an ESS, we used the first simulation method described above. Results show that there exists a narrow band in \(m - \tau\) parameter space where the mutant survives (figure 2.1A). This band exactly follows the curve (i.e., the ESSet, or evolutionarily stable set) defined by our analytical solution, equation (2.3a). In figure 2.1, we see that mutant abundance was greatest when the mutant also used the optimal strategy. In these cases, it is evident that the fitness of the mutant and the resident were equal, as reflected by the final population values. Simply, the mutant’s final abundance relative to the resident’s neither increased nor decreased from the initial relative abundance. That is to say, since the mutant was introduced at abundances of 1 into both patches one and two with resident abundances of 20 and 10, resident final abundance should have been reduced to approximately \(\frac{20}{21} \times 20 + \frac{10}{11} \times 10 \approx 28.14\), as confirmed by figure 2.1A.

Conversely, when a mutant was playing the optimal strategy, the resident’s best response is also to play \((m^*, \tau^*)\) (figure 2.1, panel B). Thus, the optimal strategy is a strict Nash equilibrium. Furthermore, a mutant could not increase against a resident playing \((m^*, \tau^*)\) since a mutant’s fitness was never greater than a resident’s fitness when the resident played the optimal strategy.

When we extended the integration time by six orders of magnitude, we observed that mutant abundances continued to decrease for strategies nearby the optimal strategy, reaching abundances
on the order of $10^{-4}$, which suggests that in the long-term, all mutant strategies other than the optimal strategy may go extinct. In sum, with regard to the ESS criterion above, though the mutant in some cases was not completely eliminated, the results (figure 2.1) show that the resident’s best response is to play an ESS candidate, and a mutant could not increase in relative abundance when the resident played an ESS candidate.

### 2.3.3 Convergence stability of the ESS

Our information-use strategy is two-dimensional and thus both strategy components ($m$ and $\tau$) are subject to mutation and selection. In the case of multi-trait evolution, it is possible that the act of mutation can at times force the evolution of the traits to take a suboptimal path in trait space (e.g., Dieckmann and Law, 1996; Leimar, 2001). The degree to which this path is less than optimal can be influenced by the correlation between the change of one trait and the change of another trait due to a single mutation (Dieckmann and Law, 1996, and references therein). Thus, one cannot assess the convergence stability of a multidimensional trait by examining the stability of each trait independently (e.g., Abrams et al., 1993; Marrow et al., 1996; Dieckmann and Law, 1996; Brown et al., 2007; Apaloo and Butler, 2009; Leimar, 2009). For this reason, in order to determine the convergence stability of the optimal strategy ($m^*, \tau^*$), we must consider the stability of $m^*$ and $\tau^*$ in tandem.

We follow the methods of Abrams et al. (1993) and rely upon the stability criteria therein (their Appendix 2) to show convergence stability of the ESS. This is the two-dimensional equivalent to the convergence criteria (1.5) presented in chapter 1. We re-derive this in appendix A for completeness, and these criteria are represented in the text as (2.4) and (2.5).

Without commenting on the specifics of the mutation, we assume that $m$ and $\tau$ are continuous quantitative traits with additive genetic variances $g_{m,m}$ and $g_{\tau,\tau}$. Since we assumed that $m$ and $\tau$ could vary independently of each other, we assume that the traits are not genetically linked, in other words, that the covariances between these traits, $g_{m,\tau}$ and $g_{\tau,m}$, are equal to zero. Let $F$ represent the fitness of a mutant. As mentioned in section 2.2.1, when we speak of the “fitness” of
Figure 2.1: Final resident population abundances in the two types of simulations used to establish candidate strategies as ESSs. (A): final resident abundances after pairwise invasion by mutant. Resident playing an ESS candidate: $m^*_R = 0.3$, $\tau^*_R = 0$. Mutant playing various $(m_M, \tau_M)$ strategies; (B): final resident abundances after pairwise invasion by a mutant playing an ESS candidate: $m^*_M = 0.3$, $\tau^*_M = 0$. Resident playing various $(m_R, \tau_R)$ strategies. Parameter values are given in table 2.1; numerical procedures are described in the text. The scale bars indicate the final abundance of the resident across both patches combined (i.e., $N_1 + N_2$). With the parameter values used, the carrying capacity of the entire system is 30 units.
the resident or mutant, we are referring to the relative replication success of that species variant.

In our notation, the two inequalities that must hold for \((m^*, \tau^*)\) to be convergence stable are (inequalities A2.4 and A2.5 of Abrams et al. (1993, pg. 485)):

\[
F_{mm} g_{m,m} + (F_{\tau m} + F_{m \tau}) g_{m,\tau} + F_{\tau \tau} g_{\tau,\tau} < 0 \tag{2.4}
\]

\[
(g_{m,m} g_{\tau,\tau} - (g_{m,\tau})^2) (F_{mm} F_{\tau \tau} - F_{m \tau} F_{\tau m}) > 0 \tag{2.5}
\]

where \(F\) is the fitness of a mutant (we use mutant population abundance as a proxy for fitness here), \(F_{m \tau} \equiv \frac{\partial^2 F}{\partial m \partial \tau}\) evaluated at \(m_M = m_R = m^*, \tau_M = \tau_R = \tau^*,\) and \(g_{m,\tau} = g_{\tau,m}\).

We found that the stability conditions, (2.4) and (2.5), were satisfied for every case we examined. Furthermore, if we were to remove the zero covariance assumption, our results still held as long as \(g_{m,m} g_{\tau,\tau} - (g_{m,\tau})^2 > 0\), appendix B. We include the results of one particular and representative case in appendix B.

2.3.4 How costs change the strategies favored by selection

Costs will cause equilibrium population values to be lower than in the absence of costs; that is, at equilibrium, a monomorphic population will be below carrying capacity in at least one patch due to the losses from the system imposed by the costs. To find fitness maximizing strategies in the presence of costs, again we begin by solving for a strategy that leads to an IFD by letting \(\gamma = \frac{N_1}{K_1} = \frac{N_2}{K_2}\), where \(0 \leq \gamma \leq 1\) (note that necessarily, \(\bar{N} = 0\)). For any distribution satisfying \(\frac{N_1}{K_1} = \frac{N_2}{K_2}\), we have \(f(N_1; K_1) = f(N_2; K_2) = r(1 - \gamma)\). At such a distribution, no organism in the system can improve its fitness by moving to another location, so we have an IFD (even if carrying capacity is not reached). The quantity \(\gamma\) represents the proportion of carrying capacity utilized at the IFD. When \(\gamma = 1\), both patches are at carrying capacity, and we recover the original optimal strategy without costs, which is not invadable. When \(\gamma < 1\), both patches are below carrying capacity at the ecological equilibrium.

Since we considered two kinds of costs (travel costs and sensory machinery costs, for convenience both are denoted by \(k\)), we calculate \(\gamma_t\) (\(t\) for travel costs) and \(\gamma_s\) (\(s\) for sensory machinery...
costs) in appendix B.1 and list them here:

\[
\gamma_t = 1 - k \frac{d}{r} \frac{K_1(2 - k)}{(K_1 + K_2) - kK_2} \tag{2.6a}
\]

\[
\gamma_s = 1 - k \frac{d}{r} \frac{(1 + K_1/K_2)}{1 - \tau^*} \tag{2.6b}
\]

Several observations follow directly from these formulas. \(\gamma_t\) and \(\gamma_s\) are similar in that: (1) both quantities increase as the intrinsic growth rate \(r\) increases and also as \(K_2\) increases and patches become more similar, and (2) both quantities decrease as costs, \(k\), increase and also as diffusion, \(d\), increases. On the other hand, and important to note, \(\gamma_t\) and \(\gamma_s\) differ by comparison since \(\gamma_t\) is not a function of \(\tau^*\). The reason for this is that by solving for (2.6a), \(m^*\) and \((1 - \tau^*)\) drop out of this expression. This leads us to conclude that \(m^*\) has no effect on the proportion of carrying capacity used by an organism playing the optimal strategy when travel costs are considered. Note that (2.6b) could be rewritten as \(\gamma_s = 1 - \frac{K}{r} \cdot m^*\), equation (B.14b), to show its explicit dependence on \(m^*\).

Heuristically, the reason that \(\gamma_t\) does not depend on \(m^*\) (or \(\tau^*\)) is that travel costs do not affect the per capita growth rate in each patch. After some algebra, we can rewrite the equilibrium equations for the system with travel costs, (B.11), as

\[
0 = \dot{N}_1 = r\gamma_1 N_1^* + (1 - k)N_2^*(d + m^*(1 - \tau^*)\tilde{K})
\]

\[
0 = \dot{N}_2 = r\gamma_2 N_2^* + (1 - k)N_1^*d
\]

where \(\gamma_1 := 1 - d - \gamma\) and \(\gamma_2 := 1 - (d + m^*(1 - \tau^*)\tilde{K}) - \gamma\) are not functions of \(k\). Note that \(r\gamma_i\) represents the per capita growth rate in patch \(i\) and the other terms represent immigration. In contrast, with sensory machinery costs, we can rewrite the equilibrium equations, (B.13), as

\[
0 = \dot{N}_1 = r\gamma(k) N_1^* - d(N_1^* - N_2^*) + m^*(1 - \tau^*)\tilde{K} N_2^*
\]

\[
0 = \dot{N}_2 = r\gamma(k) N_2^* + d(N_1^* - N_2^*) - m^*(1 - \tau^*)\tilde{K} N_2^*
\]

where \(\gamma(k) := 1 - \frac{m^*k}{r} - \gamma\) is a function of \(k\). In this case, the per capita growth rate in each patch depends directly on \(m^*k\), so the ability of organisms to use resources in each patch must also depend directly on \(m^*\).
We have represented costs in two intuitive but different ways, and below we contrast the differences in the ways that these costs change the movement strategies favored by selection. The simulation methods used are of the first type mentioned above in section 2.2.3.

2.3.4.1 Costs of traveling between patches

The strategies that lead to an IFD in the presence of travel costs are given by equation (B.12a). These strategies differs from those predicted by the model without costs, equations (2.3), but define a qualitatively similar curve in \( m - \tau \) parameter space. This can be seen by comparing the expression for \( m^* \) in the presence of travel costs (equation (B.12a)) with the expression for \( m^* \) in the absence of costs (equation (2.3a)). They differ by a multiplicative term that, for the parameter values we examined, varied from 0.931 (\( k = 0.1 \)) to 0.999 (\( k = 0.001 \)). Thus, for a fixed \( \tau \), the strategy that leads to the IFD in the presence of travel costs will have a comparatively lower level of strength of response to differences in patch qualities (i.e., a lower value of \( m^* \)). As mentioned above, the derivation of \( \gamma_t \) (equation (B.12b)) reveals that the level of resource use (\( \gamma_t \)) does not depend directly on \( \tau \). Thus, we expect that there may exist a set of \((m^*, \tau^*)\) strategies that offer equivalent fitness. We confirmed this via simulations (results not shown).

The ability of a mutant to increase depends on both the value of \( k \) and the proximity of the mutant strategy to the ESS candidate defined by equation (B.12a). For all values of \( k \) that we examined, mutant strategies can increase only when, for a given value of \( \tau_M \), the corresponding value of \( m_M \) is less than the calculated value of \( m^* \) given by equation (B.12a). Furthermore, for a fixed \( \tau_M = \tau_R = \tau^* \), mutant fitness decreases as \( m^* - m_M \) increases. For moderate values of \( k \), e.g., \( k = 0.01 \), mutant strategies can increase in abundance in a small region below this curve. For larger values of \( k \), e.g., \( k = 0.1 \), the range of \( m_M \) values for which the mutant can increase is greater, mutant abundances increase to a greater extent, and mutant strategies closest to the curve outcompete, but do not completely displace, the resident (figure 2.2).
Figure 2.2: Final resident abundance after pairwise invasion by mutant in the model with travel costs. $m^*_R = 0.3$, $\tau^*_R = 0$. (A): $k = 0.01$; (B): $k = 0.1$. The darkest areas indicate mutant strategies that successfully invaded and largely displaced the resident. As costs increase (from panel (A) to panel (B)), the range of successful mutant strategies increases.
2.3.4.2 Costs of developing and maintaining sensory machinery

When examining the results with sensory machinery costs, we were surprised to discover that the optimal strategy that led to an IFD in the absence of costs, equation (2.3a), remains the same in the presence of costs (equation (B.14a)). However, this optimal strategy will not lead to the use of all of the available resources if $\gamma_s < 1$ and so a resident playing this strategy may be vulnerable to invasion. Higher values of $\gamma_s$, equation (2.6b), indicate that fewer resources remain for an invading mutant to exploit, so we hypothesized that selection would favor resident strategies that lead to higher values of $\gamma_s$. Inspection of equation (2.6b) reveals that higher values of $\gamma_s$ can be achieved by lower values of $\tau$. Hence, we predicted that $\tau^* = 0$ would always be the best $(m^*, \tau^*)$ strategy when sensory machinery costs were considered, in contrast to the case above. That is, we predicted that ignoring fitness information and using only habitat information would be the most adaptive strategy. We verified this prediction through numerical simulation by competing two different $(m^*, \tau^*)$ strategies (i.e., two strategies that can each produce an IFD) against one another. The strategy with the lower value of $\tau^*$ could successfully invade and was also resistant to invasion by $(m^*, \tau^*)$ strategies with higher values of $\tau^*$.

The magnitude of sensory machinery costs affects the ability of a mutant to invade. For small costs (e.g., $k = 0.001$), the resident can be displaced when the mutant is playing a value of $\tau_M$ smaller than the resident’s $\tau_R = \tau^*$ and a value of $m_M$ nearby the value of $m^*$ given by (B.14a). For example, when the resident is playing $\tau^*_R = 0.5$, $m^*_R = 0.6$, a mutant with a value of $\tau_M = 0.4$ can displace the resident when $m_M = 0.45$ or $m_M = 0.50$. For larger costs (e.g., $k = 0.01$, figure 2.3), the mutant’s abundance increases for values of $m$ and $\tau$ on either side of the ESSet defined by (B.14a). For extremely large costs, e.g., $k = 0.1$, the mutant can nearly displace the resident for all values of $m_M$ and $\tau_M$ when $m_M < m_R = m^*$. Furthermore, when we competed resident $(m^*_R, \tau^*_R)$ strategies pairwise versus a range of mutant strategies, the best resident strategies were $(m^*_R, \tau^*_R) = (m^*, 0)$ (figure 2.4). In no cases could a mutant with $m_M \geq m_R$ increase in abundance.

Collectively, these results indicate that costs make it impossible for a single strategy that
would by itself lead to equal fitnesses between patches to exclude all other strategies. Additionally, when costs become large enough, cost-minimizing strategies that do not lead to an IFD can out-compete strategies that do lead to an IFD. Finally, while a range of strategies satisfying equation (B.14a) can lead to IFDs, the IFD that is closest to system carrying capacity is achieved uniquely by the strategy employing $\tau^* = 0$, that is, the strategy that ignores fitness information and uses exclusively habitat information.

2.4 Discussion

Here we first discuss how our model synthesizes several important results of previous investigations into the evolution of dispersal. We then discuss the novel aspects of our results and the ecological implications therein.

2.4.1 Synthesis of existing results on habitat selection

While a number of our results are not novel, it is indicative of the robustness and generality of our modeling approach that we are able to bring together many previously obtained results. Specifically, we are able to reproduce results from a wide variety of dissimilar models that con-
Figure 2.4: Final resident abundances after invasion by a mutant in the model with developmental and maintenance costs of sensory machinery. \( m_R = m^*, \tau_R = \tau^*, k = 0.001 \). \( \tau_R \) values are: (A) \( \tau_R = 0 \), (B) \( \tau_R = 0.2 \), (C) \( \tau_R = 0.5 \), (D) \( \tau_R = 0.8 \). Interpretation of shading as in figure 2.2.
sidered random and/or habitat-dependent movement in temporally constant but spatially varying environments.

When organisms disperse unconditionally, it has been shown that (under conditions met here) there is selection for a lesser diffusion rate (Hastings, 1983; Holt, 1985; McPeek and Holt, 1992, among others); furthermore, no dispersal is the only ESS. If we were to allow \( d \) to evolve, then from equation (2.3a), one could solve for \( d^* \), to yield an unconditional movement strategy. By definition, unconditional dispersers do not act upon any fitness or environmental cues. This equates to \( m = 0 \) which leads to the ESS of \( d^* = 0 \), in agreement with previous work.

The landmark paper by McPeek and Holt (1992) considered both unconditional and conditional dispersal in a two-patch model. They noted that, concerning the genotypes associated with evolutionarily stable strategies, any number of genotypes with patch-specific dispersal propensities in ratios inversely proportional to the ratio of the carrying capacities can coexist (McPeek and Holt, 1992, pg. 1015). In short, there exists a set of dispersal strategies (rather than a unique strategy) that is neutrally stable. As figure 2.1 suggests, any number of strategies satisfying equations (2.3) can coexist with any other strategies also satisfying equations (2.3). Additionally, we see that our optimal strategy’s patch-specific dispersal propensities occur in ratios inversely proportional to the ratio of the carrying capacities. Clearly, when the optimal strategy is played, the movement rate from patch 1 into patch 2 is \( d \), and the movement rate from patch 2 into patch 1 is \( d \cdot \frac{K_2}{K_1} \). Thus, the ratio of dispersal rates from patch 1 to dispersal rates from patch 2 is \( \frac{K_2}{K_1} \) (and, incidentally, mirrors the equality condition in equation 2, page 1015, of McPeek and Holt (1992)).

General results from continuous space models should hold analogously for discrete space models such as ours. As an example, we present one result from a partial differential equation model that holds analogously in our model. Cantrell et al. (2006) found that when two variants of a species that differ only in dispersal strategies compete, where one variant disperses diffusively and the other disperses both diffusively and up a resource gradient, the second variant can outcompete the first even when it has a higher rate of diffusive movement. Recall that for our model, conditional movement via habitat-dependent cues is achieved by setting \( \tau = 0 \) in equations (2.1) and (2.2),
and thus, in our context, conditional movement from patch 2 to patch 1 is analogous to moving up a resource gradient. We can label two variants $a$ and $b$ and denote their parameter values with the appropriate subscripts. Let variant $a$ disperse unconditionally and variant $b$ disperse both unconditionally and up the resource gradient. Setting $\tau^*$ to zero in equation (2.3a) yields a value of $m = m^* = d(1 + \frac{K_1}{K_2})$. Then, it is easily seen that $d_b > d_a > 0$ implies $m_b^* > m_a^* > 0$. Since variant $a$ with strategy $d_a > 0$ and $m_a = 0$ is not playing the optimal strategy ($m_a \neq m_a^*$), the variant with the second strategy can invade if its strategy is closer to the optimal.

2.4.2 Contrasting travel costs with sensory development costs

We found that the addition of costs fundamentally changed the evolutionary stability of those strategies that would have, in the absence of costs, led to an IFD. For both types of costs, organisms using strategies that led to the IFD were unable to fully utilize resources in either patch. This allowed organisms using a different strategy to invade, but the set of successful invasion strategies varied depending on the types of costs considered. With the addition of travel costs, strategies with a moderately lower strength of response to assessed differences between patches relative to the ESS candidate (B.12a) could outcompete any IFD strategy. The particular blend of information used by either the resident or the mutant did not affect these results. By contrast, with the addition of the costs of developing or maintaining sensory machinery, mutants with both moderately higher and lower strength of response to assessed differences between patches relative to the ESS candidate (B.14a) could invade. Furthermore, in contrast to the travel costs model, the range of successful mutant strategies depended fundamentally on the resident’s information-use strategy.

2.4.3 Why fitness-dependent movement may be maladaptive

In the presence of suboptimal movement, moving up a fitness gradient does not maximize fitness and as such cannot be an ESS. In other words, being more sensitive to fitness differences will not necessarily increase one’s fitness! While we are not the first to suggest this paradoxical hypothesis (see, e.g., Hastings, 1983; McPeek and Holt, 1992; Krivan et al., 2008, among others),
fitness-based movement is still generally assumed to be adaptive. Furthermore, previous works have not directly competed fitness-based movement against habitat-based movement, and our work thus provides the most complete and rigorous test of this hypothesis to date. We have been able to show that, for all fixed values of $m$, as the magnitude of suboptimal movement (i.e., $d$) increases, fitness-dependent movement is increasingly selected against. This can be explained by recognizing that in contrast to the normalized fitness difference between patches ($\tilde{N}$), the normalized carrying capacity difference between patches ($\tilde{K}$) does not change as consumer distributions approach the IFD. Thus, when non-IFD movements can be approximated by discrete diffusion, the term $\tilde{K}$ contains more information on where to go to maximize overall fitness (see Flaxman and Lou 2009 for a similar conclusion in a predator-prey model). Moreover, when two patches vary greatly in resource quality ($K_1 >> K_2$), it becomes increasingly likely that habitat-dependent movement will be selected for. This follows from equation (2.3b) and makes intuitive sense, since when resources vary greatly from one patch to another, organisms ought to pay increased attention to these differences.

The parameter $m$ represents sensitivity to information (or alternatively the rate at which information is acted upon) and should, realistically, be finite. However, strict fitness-dependent movement ($\tau = 1$) is selected for only when $m = \infty$ (see also Cressman and Krivan, 2006; Cantrell et al., 2008), which is not biologically possible. One could even argue that lower values of $m$ might be advantageous, in the sense that lower values of $m$ translate to less of an energy expense on directed movement or less of an investment in environmental sensory functionality. Our novel analysis on costs supports the hypothesis that organisms should, in the presence of sensory machinery costs, move based on information regarding relative habitat differences rather than relative fitness differences.

2.4.4 Concluding remarks

Through the use of a simple, single-species movement model, we were able to identify analytically a convergent evolutionarily stable movement strategy. By modeling movement using general local movement cues, we were able to compete two types of information-use strategies to discover
that movement based solely on information about fitness is not generally adaptive, which should, at
the least, raise questions about the implementation of fitness-based movement in habitat selection
models. Our analyses also indicate that real organisms do not need to “know” their fitness in
order to behave in ways that maximize it; in fact, even if fitness is known to an organism, natural
selection may actually favor the use of simpler information and can shape the way organisms use
this information to overcome the constraints that they face.
Chapter 3

Stability analysis of a habitat selection model incorporating adaptive information use

3.1 Introduction

The dispersal of organisms can be an important factor in determining the complexity and stability of ecological food webs (van Baalen and Sabelis, 1993; Nathan, 2008; Schreiber, 2010). Many species use available information to determine the direction and rate at which they move through their environment. Organisms that can act upon multiple sources of available information to guide their movements must in some sense “choose” the best sources of information to which to pay attention. Discovering how organisms might use different general sources of information to guide movement is critical to understanding how movement affects the complexity of food webs (Amarasekare, 2010).

The study of single-species optimal dispersal has generated a rich literature (see review by Lou, 2008). For example, in spatially heterogeneous but temporally constant environments, dispersal should be selected against (Hastings, 1983; Holt, 1985; Dockery et al., 1998). This presumes that organisms move unconditionally, without regard for environmental conditions. On the other hand, when organisms use information about their environment to guide movement (i.e., “conditional movement”), natural selection may favor certain dispersal strategies over others (McPeek and Holt, 1992; Holt and McPeek, 1996; Kirkland et al., 2006; Padron and Trevisan, 2006; Cantrell et al., 2007a; Galanthay and Flaxman, 2012). A conditional movement strategy that is often evolutionarily advantageous in temporally constant environments is one that leads to “balanced
dispersal" (McPeek and Holt, 1992). When dispersal is balanced, the number of immigrants to a location is offset exactly by the number of emigrants from that location. If the single-species population dynamics are globally attracted to an equilibrium in the absence of movement, then the population will reach this same equilibrium with balanced dispersal. Thus, organisms using such a strategy will be distributed so that the net growth rate in all patches is equivalent and equal to zero. At this type of equilibrium, organisms are in an ideal free distribution (Fretwell and Lucas, 1969).

At small spatial scales, ideal free distribution (hereafter, “IFD”) theory has been used to predict optimal habitat selection (Fretwell and Lucas, 1969). The theory describes how equally competitive animals with perfect information and the freedom to act upon that information should distribute themselves in a patchy environment (see Cosner, 2005, for an extension to continuous space). The IFD has generally been studied as an equilibrium state in which Darwinian fitness across patches of habitat is equal (but see Křivan, 1997). The theory has attracted much attention (see reviews by Kennedy and Gray, 1993; Milinski, 1994; Tregenza, 1995; Křivan et al., 2008; Abrams, 2010) and received empirical support (e.g., Milinski, 1979; Diffendorfer, 1998) at various spatial scales.

IFD theory assumes that organisms have perfect information and move instantaneously. However, real animals may be constrained by perceptual limitations or otherwise possess imperfect information about their environment (Hakoyama and Iguchi, 1997; Kennedy and Gray, 1997). These constraints might affect how organisms are able to distribute themselves. Theoretical studies of optimal foraging behavior have shown that these constraints will cause individuals to be less abundant in patches of higher quality than would otherwise be predicted by the IFD (Spencer et al., 1996; Hugie and Grand, 1998; Ranta et al., 1999). IFD theory also assumes that animals move between patches without cost. When organisms are forced to pay a cost to move between patches that differ in resource quality, organism abundances across patches become more similar (shown empirically by Morris (1987); Korona (1990); Kennedy and Gray (1997), and theoretically by Matsumura et al. (2010)). That is, organisms tend to “undermatch” available resources in the patch with more re-
sources (Parker, 1978). Over time, this can lead to source-sink dynamics (Pulliam, 1988) where instantaneous per capita fitness is positive in the higher quality patch. This phenomenon has also been observed in multi-trophic models (e.g., consumer-resource and predator-prey-resource) with population dynamics when consumer movement alone is considered (DeAngelis et al., 2011).

In the previous chapter, we studied a single-species, two-patch model to investigate the types of movement rules that might be evolutionarily stable for organisms constrained by imperfect information and subject to various costs. The model had features of previous partial differential equation models (Belgacem and Cosner, 1995; Cantrell et al., 2008; Flaxman and Lou, 2009; Cantrell et al., 2010; Averill et al., 2012) and ordinary differential equation models (Freedman and Waltman, 1977; Hastings, 1982; Holt, 1985; Freedman et al., 1986). The simplest of the latter models has the general form

\[
\frac{dN_1}{dt} = N_1 f_1(N_1) - h_1(N_1; \epsilon) + h_2(N_2; \epsilon) \tag{3.1a}
\]

\[
\frac{dN_2}{dt} = N_2 f_2(N_2) + h_1(N_1; \epsilon) - h_2(N_2; \epsilon) \tag{3.1b}
\]

where \(N_i\) represents species abundance in patch \(i\) and \(f_i\) is the per capita growth rate in patch \(i\) (i.e., instantaneous fitness). The function \(h_i\) regulates movement from patch \(i\), and \(\epsilon\) is a parameter that has alternatively represented either barrier strength to movement between patches (Freedman and Waltman, 1977; Freedman et al., 1986) or discrete diffusion rate (Hastings, 1982; Holt, 1985).

The state variables of the model (3.1) represent organism abundance, so we are generally interested in determining the existence, uniqueness, and stability of a non-trivial, non-negative equilibrium. Freedman and Waltman (1977) proved, in the case when the per capita fitness function \(f\) is the logistic growth function (e.g., \(f_i(N_i) = r_i(1 - \frac{N_i}{K_i})\)), that there exists a positive, asymptotically stable equilibrium of (3.1). More generally, for a density-dependent function \(f\), with \(f_i(0) = 0, f_i(K_i) = 0\), and taking \(h_i(N_i; \epsilon) = \epsilon N_i\), Holt (1985) proved that (3.1) has a unique, positive, globally asymptotically stable equilibrium.
Freedman et al. (1986) studied the existence and stability of equilibria of a similar model

\[
\frac{d N_1}{dt} = N_1 f_1(N_1) - h_1(N_1; \epsilon_1) + p_{21} h_2(N_2; \epsilon_2) \quad (3.2a)
\]

\[
\frac{d N_2}{dt} = N_2 f_2(N_2) + p_{12} h_1(N_1; \epsilon_1) - h_2(N_2; \epsilon_2) \quad (3.2b)
\]

This differs from (3.1) in that \( \epsilon \) is patch-specific and \( p_{ji} \leq 1 \) represents the probability that organisms migrating from patch \( j \) arrive safely at the destination patch \( i \). Freedman et al. (1986) obtained conditions for which a non-trivial, positive equilibrium exists, and they proved that if the equilibrium is unique, then it is globally asymptotically stable.

In the previous chapter, we extended model (3.2) by allowing \( h_i \) to depend on both \( N_1 \) and \( N_2 \). In doing this, we were able to ask: if organisms have access to information about resources and fitness, what information-use strategies to guide movement might be adaptive, and how might these strategies be affected by costs? Although the numerical results confirmed that certain strategies were adaptive, we presented no mathematical proof. Furthermore, we found these strategies by assuming that the system had a globally stable equilibrium. Although numerical explorations suggested this to be the case, again we presented no proof. Such an analysis is imperative because by including fitness-based movement (cf. Abrams, 2007), previous results on the existence and stability of equilibrium points do not immediately apply.

One of the goals of this chapter is to provide the mathematical justification for some of the previous chapter’s assumptions and conclusions. These results may be more broadly applicable to studying questions of adaptive movement in patchy environments in the presence of perceptual constraints and travel costs. In doing so, we extend previous mathematical treatments of two-patch population dynamical models with movement and demonstrate effective mathematical techniques that allow more rigorous study of these types of systems. We will prove that the single-species model (3.3) has a positive equilibrium and give sufficient conditions for uniqueness and global asymptotic stability. We are motivated to do this, in part, because it is well-known that if this equilibrium exists and is globally asymptotically stable, then one can analyze the evolutionary stability of movement strategies using simple ideas from adaptive dynamics (Metz et al., 1996; Dieckmann and
Law, 1996; Geritz et al., 2002). We intend to show that certain adaptive strategies are attractors of the underlying evolutionary dynamics. Furthermore, we prove that when movement is costly, the new adaptive strategy is to reduce the movement rate until instantaneous fitness is zero in one patch.

To determine whether a strategy is adaptive, we follow the modeling approach of the previous chapter and consider a four-dimensional model that represents the change in abundances of a “resident” and “mutant” species in a two-patch environment (Dieckmann and Law, 1996; Geritz et al., 1998; Diekmann, 2004; Kisdi and Geritz, 2010). The mutant is a second species (or variant of the first) that is identical to the resident except perhaps for its movement strategy. We assume that the rate of mutations is slow enough so that the ecological dynamics reach equilibrium prior to the introduction of a new mutant. Furthermore, we assume that two species will exist simultaneously at equilibrium only if either species can increase when rare in the presence of the other species, similar to Geritz et al. (1998). Thus, no more than two species will ever exist in the system at any single time.

We rely on the concept of the evolutionarily stable strategy to determine the existence of optimal strategies. A strategy is an evolutionarily stable strategy (hereafter, “ESS”) if a mutant playing a different strategy cannot increase when rare (Maynard Smith, 1982). Evolutionary stability does not imply convergence stability, since it is well known that a strategy may be an ESS but not an attractor of the evolutionary dynamics (Eshel and Motro, 1981). Since we are interested in describing strategies that are attainable through the mechanism of natural selection, we will consider not only the evolutionary stability but also the convergence stability of a strategy (defined in chapter 1). We presented sufficient conditions for convergence stability in chapter 1 for a one-dimensional strategy (1.5) and again in chapter 2 for a two-dimensional strategy, (2.4) and (2.5). It is worth mentioning that convergence stability in higher-dimensional parameter spaces has been defined variously by several authors (e.g., Abrams et al., 1993; Leimar, 2005, 2009; Apaloo and Butler, 2009). In the review by Apaloo and Butler (2009), “m* is a convergence stable strategy if it is a locally asymptotically stable equilibrium point of an adaptive strategy dynamics” (Apaloo
and Butler, 2009, pg. 640). If a strategy is both an ESS and convergence stable, we refer to it as a continuously stable strategy (hereafter, “CSS”) (Eshel and Motro, 1981). When movement is cost-free, the CSS leads to an IFD. Interestingly, when movement is costly, the CSS does not lead to an IFD, rather, the adaptive strategy is to reduce the movement rate until instantaneous fitness is exactly zero in only one patch.

Our analysis proceeds as follows. In section 3.2, we re-introduce two model systems (resident-only and resident-mutant) that describe population dynamics and movement between two patches. In section 3.3, we give sufficient conditions for the single-species model to have a unique, globally asymptotically stable positive equilibrium. In section 3.4, we prove that the information-use strategy from chapter 2 is a CSS. Finally, in section 3.5, we consider how travel costs affect the adaptive strategy from section 3.4. We show that the strategy from section 3.4 is no longer an ESS, but prove that there exists a fundamentally different adaptive strategy that is both an ESS and convergence stable, hence a CSS.

### 3.2 The model

For convenience, we write here the model previously introduced in chapter 2 and found in appendix B, (B.11). The following model represents the population dynamics of a single species in a two-patch environment.

\[
\dot{N}_1 = N_1 f_1(N_1) - d N_1 + (1-k)(d + m(\tau \max(0, \tilde{N}) + (1-\tau)\bar{K})))N_2
- m\tau \max(0, -\tilde{N})N_1
\]

\[
\dot{N}_2 = N_2 f_2(N_2) + (1-k)d N_1 - (d + m(\tau \max(0, \tilde{N}) + (1-\tau)\bar{K})))N_2
+ (1-k)m\tau \max(0, -\tilde{N})N_1
\]

where

\[
\tilde{N} = \frac{f_1(N_1) - f_2(N_2)}{r(N_1/K_1 + N_2/K_2)} = \frac{\frac{N_2}{K_2} - \frac{N_1}{K_1}}{\frac{N_2}{K_2} + \frac{N_1}{K_1}} = \frac{K_1 N_2 - K_2 N_1}{K_1 N_2 + K_2 N_1},
\]

\[
\bar{K} = \frac{K_1 - K_2}{K_1 + K_2},
\]
and $\tilde{N}$ and $\tilde{K}$ represent differential fitness and resource information respectively. We model $\tilde{N}$ with a specific nonlinear form that is more sensitive to changes in abundance when abundances in either patch are small (e.g., Abrams et al., 2007).

We assume that $r, d > 0, K_1 > K_2,$ and $k \in [0,1)$. Together, $m$ and $\tau$ represent a two-dimensional information-use strategy, $(m, \tau)$, where $m \geq 0$ and $\tau \in [0,1]$. When organisms travel without cost (i.e., $k = 0$), there exists a special pair of $(m, \tau)$ values at which $N_i = K_i$ at equilibrium (Galanthay and Flaxman, 2012). These values are given by the relation

$$m^* = \frac{d(1 + \frac{K_1}{K_2})}{1 - \tau^*}$$

(3.5)

We will call $(m^*, \tau^*)$ the optimal strategy. (3.5) defines a curve in $m - \tau$ parameter space, so when describing this relation in parameter space, we will refer to (3.5) as the ESSet, as in section 2.3.2. For analytic tractability, we will occasionally set $\tau = 0$. Then, the optimal strategy when $k = 0$ simplifies to $(m^*, 0)$ where $m^* = d(1 + \frac{K_1}{K_2})$.

To study the evolutionary stability of information-use strategies $(m, \tau)$, we consider a four-dimensional system analogous to (3.3), namely

$$\dot{N}_1 = N_1 g_1(N_1, M_1; K_1) - dN_1 + (1 - k)(d + m_R(\tau_R \max(0, \tilde{N}) + (1 - \tau_R)\tilde{K}))N_2$$

$$- m_R \tau_R \max(0, -\tilde{N})N_1$$

(3.6a)

$$\dot{N}_2 = N_2 g_2(N_2, M_2; K_2) + (1 - k)dN_1 - (d + m_R(\tau_R \max(0, \tilde{N}) + (1 - \tau_R)\tilde{K}))N_2$$

$$+ (1 - k)m_R \tau_R \max(0, -\tilde{N})N_1$$

(3.6b)

$$\dot{M}_1 = M_1 g_1(M_1, N_1; K_1) - dM_1 + (1 - k)(d + m_M(\tau_M \max(0, \tilde{N}) + (1 - \tau_M)\tilde{K}))M_2$$

$$- m_M \tau_M \max(0, -\tilde{N})M_1$$

(3.6c)

$$\dot{M}_2 = M_2 g_2(M_2, N_2; K_2) + (1 - k)dM_1 - (d + m_M(\tau_M \max(0, \tilde{N}) + (1 - \tau_M)\tilde{K}))M_2$$

$$+ (1 - k)m_M \tau_M \max(0, -\tilde{N})M_1$$

(3.6d)

where $M_i$ represents mutant abundance in patch $i$, $g_i(N_i, M_i; K_i) = r(1 - \frac{N_i + M_i}{K_i})$ and now $\tilde{N} = \frac{(N_2 + M_2)/K_2 - (N_1 + M_1)/K_1}{(N_2 + M_2)/K_2 + (N_1 + M_1)/K_1}$. Since the mutant is identical to the original species except perhaps for
its strategy, all parameters apart from the strategy are identical, thus not species-specific. We represent the information-use strategies of the resident and mutant by the subscripts $R$ and $M$ respectively.

### 3.3 Analysis of the two-dimensional model

Before we consider (3.3), consider the simpler system of equations

\[
\begin{align*}
\dot{N}_1 &= r(1 - \frac{N_1}{K_1}) \cdot N_1 - dN_1 + (1 - k)(d + m\tilde{K})N_2 \\
\dot{N}_2 &= r(1 - \frac{N_2}{K_2}) \cdot N_2 + (1 - k)dN_1 - (d + m\tilde{K})N_2
\end{align*}
\] (3.7)

which is obtained from (3.3) by setting $\tau = 0$. The nullclines of this system (i.e., $\dot{N}_1 = 0$, $\dot{N}_2 = 0$) are defined implicitly by the functions $\hat{F}_i = 0$, equations (3.8). Since $d > 0$, these equations are parabolas in the $N_1 - N_2$ plane.

\[
\begin{align*}
\hat{F}_1(N_1, N_2) &= N_2^2 - K_1(1 - \frac{d}{r})N_1 - \frac{K_1}{r}(1 - k)(d + m\tilde{K})N_2 \\
\hat{F}_2(N_1, N_2) &= N_2^2 - K_2(1 - \frac{d + m\tilde{K}}{r})N_2 - \frac{K_2}{r}(1 - k)dN_1
\end{align*}
\] (3.8)

By inspection, each $\hat{F}_i = 0$ (with respect to $N_i$) has positive slope in the positive quadrant, intersects at the origin, and has positive concavity. Additionally, $\hat{F}_1 = 0$ crosses the $N_1$-axis at $(K_1(1 - \frac{d}{r}), 0)$ and $\hat{F}_2 = 0$ crosses the $N_2$-axis at $(0, K_2(1 - \frac{d + m\tilde{K}}{r}))$. Therefore, (3.7) has a unique, positive equilibrium, $E_0 = (N_1^*, N_2^*)$. Standard geometric nullcline analysis demonstrates that this equilibrium is globally asymptotically stable.

When $\tau \neq 0$, the single-species model is defined not by the simpler system (3.7) but by (3.3). We must work harder to establish that a positive equilibrium of (3.3) exists since the nullclines are no longer parabolas. Set $k = 0$ and consider the sum of equations (3.3) at equilibrium.

\[
0 = \dot{N}_1 + \dot{N}_2 = r(1 - \frac{N_1}{K_1})N_1 + r(1 - \frac{N_2}{K_2})N_2
\] (3.9)

The movement terms do not appear because in the absence of costs, emigration to one patch is exactly offset by immigration from the other patch. Equation (3.9) defines an ellipse in the $N_1 - N_2$ plane.
plane, and any equilibrium will coincide with a point at which the nullclines intersect this ellipse.

Let the implicit functions $F_i(N_1, N_2) = 0$ represent the nullclines of (3.3)

\[
F_1(N_1, N_2) = r\left(1 - \frac{N_1}{K_1}\right) \cdot N_1 - dN_1 + \left(d + m\tau \max(0, \bar{N}) + (1 - \tau)\bar{K}\right)N_2
\]
\[\quad - m\tau \max(0, -\bar{N})N_1 \tag{3.10a}\]

\[
F_2(N_1, N_2) = r\left(1 - \frac{N_2}{K_2}\right) \cdot N_2 + dN_1 - \left(d + m\tau \max(0, \bar{N}) + (1 - \tau)\bar{K}\right)N_2
\]
\[\quad + m\tau \max(0, -\bar{N})N_1 \tag{3.10b}\]

Define

\[
\mu_i(N_1, N_2) := \{F_i(N_1, N_2) = 0\}. \tag{3.11}\]

We show in lemma 1 that the locus of points given by $\mu_1(N_1, N_2)$ intersects the ellipse given by (3.9), thus a positive equilibrium of (3.3) exists.

---

**Figure 3.1:** The ellipse given by (3.9) is the dash-dot curve. $\mu_1$ is the solid line, $\mu_2$ is the dashed line, where $\mu_i$ are given in the text, (3.11). The equilibrium is given by the crossing of $\mu_1$ and $\mu_2$. Arrows give a general sense of the direction of trajectories. Parameter values for both panels are: $d = 0.1$, $m = 0.5$, $\tau = 0.1$. (A): $r = 1$, (B): $r = 0.14$. Note that $r > d + m\tau$ in panel (A), and $r < d + m\tau$ in panel (B).

**Lemma 1.** $\mu_1(N_1, N_2)$ intersects the ellipse given by (3.9) at least once. Therefore, a positive equilibrium of (3.3), $E_0 = (N_1^*, N_2^*)$, exists.

**Proof.** We will begin by establishing the following two facts from which the conclusion of the lemma will follow summarily. First, $\mu_1$ intersects the $N_1$-axis twice, once at the origin and once at a point
whose sign depends on \((r - (d + m\tau))\). We will show that \(\mu_1\) enters the first quadrant at a point inside the ellipse given by (3.9). Second, the slope of the tangent line of \(\mu_1\) is positive throughout the positive quadrant. From these two facts, \(\mu_1\) must intersect the ellipse given by (3.9) thereby establishing the existence of a positive equilibrium of (3.3).

\(\mu_1(N_1, N_2)\) intersects the \(N_1\)-axis when \(N_2 = 0\). Recall from (3.4) that \(\tilde{N}(N_1 > 0, N_2 = 0) = -1\). We define \(\tilde{N}|_{(N_1=0, N_2=0)} = 0\). Solving \(F_1(N_1, 0) = 0\) for \(N_1\) demonstrates that \(\mu_1\) intersects the \(N_1\)-axis when \(N_1 = 0\) and \(N_1 = K_1(1 - \frac{d + m\tau}{r})\). When \(r > d + m\tau\), \(\mu_1\) intersects the \(N_1\)-axis at a positive point interior to the ellipse. This point lies between the origin and the point \((K_1, 0)\) where the ellipse intersects the \(N_1\)-axis (figure 3.1, panel A). Taking the derivative of \(F_1(N_1, N_2) = 0\) with respect to \(N_1\) and evaluating at the point \((K_1(1 - \frac{d + m\tau}{r}), 0)\) yields

\[
N_2' = \frac{r - (d + m\tau)}{2m\tau \frac{K_1}{K_2} + d + m(1 - \tau)K} > 0
\]

where \(N_2'\) denotes \(\frac{dN_2}{dN_1}\), the slope of the tangent line of \(\mu_1\). When \(r \leq d + m\tau\), \(\mu_1\) intersects the \(N_1\)-axis at the origin and, if \(r \neq d + m\tau\), at a point on the negative \(N_1\)-axis (figure 3.1, panel B). We cannot show that the slope of the tangent line of \(\mu_1\) is positive at the origin since the derivative of \(\tilde{N}\) is undefined there. Instead, we will show that \(\mu_1\) exists inside the ellipse in the first quadrant. Assume \(r \leq d + m\tau\). Then, \(F_1(N_1, 0) < 0\) when \(N_1 > 0\) by direct evaluation of equation (3.10a). Also, \(F_1(0, N_2) > 0\) when \(N_2 > 0\). If we choose \(N_1\) and \(N_2\) small enough, then the line \(L_1\) connecting the two points \((N_1, 0)\) and \((0, N_2)\) lies entirely inside the ellipse. Since \(F_1(N_1, N_2)\) is continuous, there must exist a point \((\tilde{N}_1, \tilde{N}_2)\) that lies on the line \(L_1\) for which \(F_1(\tilde{N}_1, \tilde{N}_2) = 0\). This establishes that \(\mu_1\) exists inside the ellipse in the first quadrant.

Now we show that the tangent to \(\mu_1\) has positive slope throughout the positive quadrant. Consider the curves defined implicitly by

\[
G_i(N_1, N_2) = \frac{F_i}{N_i} = 0, \quad \text{(Holt, 1985)}.
\]

Note that if \(G_1(N_1, N_2)\) has positive slope, then the tangent to \(\mu_1\) will also have positive slope since \(N_1 > 0\). We will assume for the moment that \(\tilde{N} \geq 0\). We show that the slope of \(G_1\) is positive
by differentiating \( G_1 \) with respect to \( N_1 \) and solving for \( \frac{dN_2}{dN_1} \). Letting \( N_2' \) denote \( \frac{dN_2}{dN_1} \),

\[
\frac{dG_1}{dN_1} = 0 = - \frac{r}{K_1} + (d + m(\tau \tilde{N} + (1 - \tau) \tilde{K})) \frac{N_1 N_2' - N_2}{N_1^2} \\
+ 2m\tau \frac{N_2}{N_1} \left[- \frac{N_2}{K_1 K_2} + \frac{N_1 N_2'}{K_1 K_2} \right]/\left[ \frac{N_2}{K_2} + \frac{N_1}{K_1} \right]^2
\]

\[\Rightarrow N_2' > 0\]

Now, consider \( \tilde{N} \leq 0 \).

\[
\frac{dG_1}{dN_1} = 0 = - \frac{r}{K_1} + (d + m(1 - \tau) \tilde{K})) \frac{N_1 N_2' - N_2}{N_1^2} \\
+ 2m\tau \frac{N_2}{N_1} \left[- \frac{N_2}{K_1 K_2} + \frac{N_1 N_2'}{K_1 K_2} \right]/\left[ \frac{N_2}{K_2} + \frac{N_1}{K_1} \right]^2
\]

\[\Rightarrow N_2' > 0\]

Similarly, one could show for \( G_2 \) that \( \frac{dN_1}{dN_2} = N_1' > 0 \).

Therefore, \( \mu_1 \) enters the positive quadrant interior to the ellipse (3.9) either at the point \((0, 0)\) or \((K_1(1 - \frac{d+m\tau}{r}), 0)\). This curve has positive slope everywhere in the positive quadrant, so it must intersect the ellipse at least once. Equilibria are given by the common points of \( \mu_1 \) and (3.9) since this curve, \( \mu_1 \), consists of the points where \( \dot{N}_1 = 0 \), and the ellipse given by (3.9) consists of the points where \( \dot{N}_1 + \dot{N}_2 = 0 \). Therefore, a positive equilibrium exists. Note that the curve \( \mu_2 \) crosses the ellipse given by (3.9) at the same common set of points.

\[\Box\]

**Theorem 1.** \( N_2^* \geq \frac{K_2}{2} \) is a sufficient condition for the system of equations given by (3.3) to have a unique positive equilibrium, \( E_0 = (N_1^*, N_2^*) \), that is globally asymptotically stable.

**Proof.** Any equilibrium must lie on the ellipse given by (3.9). This ellipse has a unique vertical tangent in the positive quadrant at \((N_1, N_2) = (\frac{K_1}{2}(1 + \sqrt{1 + \frac{K_2}{K_1}}), \frac{K_2}{2})\). By lemma 1, \( G_1 \), given
by (3.12), has positive slope in the positive quadrant. Thus, if \( \mu_1 \), given by (3.11), intersects the ellipse at or above \( N_2^* = \frac{K_2}{2} \), then the equilibrium must be unique.

One can also show that \( G_2 \) has positive slope (with respect to \( N_2 \)) in the positive quadrant. Then, global stability follows from standard analysis of planar differential equation systems (e.g., Braun, 1983, pp. 426-30). Therefore, when \( N_2^* \geq \frac{K_2}{2} \), the positive equilibrium \( E_0 \) is globally asymptotically stable.

When \( k \neq 0 \), \( \dot{N}_1 + \dot{N}_2 = 0 \) is no longer an ellipse, but a locus of points (here a piecewise cubic relation). For small values of \( k \), the previous results will hold. For large values of \( k \), plots of \( \dot{N}_1 + \dot{N}_2 = 0 \) and the nullclines suggest that there exists a value of \( N_2 \) on this new locus of points above which the equilibrium will be unique and globally asymptotically stable (figure 3.2).

![Figure 3.2](image)

**Figure 3.2:** The locus of points \( \dot{N}_1 + \dot{N}_2 = 0 \) when \( k \neq 0 \) is given by the dash-dot curve. The solid line represents \( \dot{N}_1 = 0 \). The dashed line represents \( \dot{N}_2 = 0 \). Parameters: \( k = 0.1, r = 0.05, d = 0.1, m = 0.5, \tau = 0.1 \).

### 3.4 Evolutionary and convergence stability of \((m^*, \tau^*)\)

Now we consider the stability of the equilibrium \( E_1 = (N_1^*, N_2^*, 0, 0) \) for system (3.6) when \( k = 0 \). From now on, we will assume that there exists a globally asymptotically stable equilibrium, \( E_0 \), of (3.3). First, we will show when the resident is playing the optimal strategy, \((m^*, \tau^*)\) (given by (3.5)), that \((N_1^*, N_2^*, 0, 0) = (K_1, K_2, 0, 0)\) is asymptotically stable. This proves that
no other strategy can invade when the resident is playing \((m^*, \tau^*)\), in other words, \((m^*, \tau^*)\) is an ESS. Second, we will show that \((m^*, \tau^*)\) is convergence stable when the resident and mutant play strategies nearby the optimal strategy.

We can attempt to determine the local stability of the resident-only equilibrium \(E_1\) using classical linearization techniques. We consider the full system (3.6) when \(\tilde{N} \geq 0\) since the analysis for the \(\tilde{N} \leq 0\) case is analogous.

Let \(J\) denote the Jacobian of (3.6). Then, we can write \(J\) evaluated at \(E_1\) in the block-diagonal form

\[
J|_{E_1} = \begin{bmatrix} J_1 & X \\ 0 & J_2 \end{bmatrix}
\]

where \(J\) is the Jacobian of the two-species system, sometimes called the “community matrix” (e.g., Vandermeer, 1970). \(J_1\) is the same as the Jacobian of the single-species system (3.3), \(X\) is the \(2 \times 2\) matrix

\[
X = \begin{bmatrix} \frac{\partial \dot{N}_1}{\partial M_1} & \frac{\partial \dot{N}_1}{\partial M_2} \\ \frac{\partial \dot{N}_2}{\partial M_1} & \frac{\partial \dot{N}_2}{\partial M_2} \end{bmatrix},
\]

and

\[
J_2 = \begin{bmatrix} r(1 - \frac{N_1^*}{K_1}) - d & d + m_M(\tau_M \tilde{N} + (1 - \tau_M)\tilde{K}) \\ d & r(1 - \frac{N_2^*}{K_2}) - d - m_M(\tau_M \tilde{N} + (1 - \tau_M)\tilde{K}) \end{bmatrix}
\]

and is commonly referred to as the “invasion matrix.” All submatrices are evaluated at \(E_1\). Due to the block diagonal structure of \(J\), the eigenvalues of (3.13) are given by the eigenvalues of \(J_1\) and \(J_2\). The eigenvalues of \(J_1\) are negative, since \(E_0\) is asymptotically stable by assumption. Furthermore, by the Perron-Frobenius Theorem (e.g., Horn and Johnson, 1999), the matrix \(J_2 + \hat{d}I\) (\(\hat{d}\) a positive constant) has a unique largest eigenvalue, \(\lambda^{(1)}\), and the associated eigenvector \(v^{(1)}\) can be chosen to have strictly positive entries. Thus, there will also be a unique largest eigenvalue for \(J_2\) with the same associated eigenvector \(v^{(1)}\) as for \(J_2 + \hat{d}I\) (as in DeAngelis et al., 2011). Due to \(v^{(1)}\) having positive components in the direction of \(M_1\) and \(M_2\), it follows that the sign of the largest
eigenvalue of $J_2$ will determine whether or not the mutant can increase when rare. If the sign of this largest eigenvalue is positive (respectively, negative) then the mutant can (cannot) increase when rare. Thus, to prove that $E_1$ is linearly asymptotically stable, we must show that the eigenvalues of $J_2$ are strictly negative. Unfortunately, for single-species two-patch systems, when per-capita fitness equals zero in both patches at equilibrium and there are no movement costs, the largest eigenvalue will be zero. This follows from (3.14) by letting $f_i = 0$ and noticing that the first row is a negative one multiple of the second row. Given that the equilibrium is not asymptotically stable (i.e., $\lambda^{(1)} = 0$), we can apply center manifold reduction techniques (e.g., Meiss, 2007) to determine local evolutionary stability. When $\tau = 0$, the calculation is tractable, and we can prove that a resident playing $(m^*, 0)$ can resist invasion by a mutant with a value of $m_M \neq m^*$ (Appendix C). In fact, we can prove global evolutionary stability.

Consider the resident-mutant system (3.6) when the resident is playing the optimal strategy. Recall from the single-species system (3.3) that $(m, \tau) = (m^*, \tau^*)$ implies $(N_1^*, N_2^*) = (K_1, K_2)$, which is globally asymptotically stable. We show here when $m_R = m^*$, $m_M \neq m^*$, and $\tau_R = \tau^* = 0$ that $(N_1^*, N_2^*, M_1^*, M_2^*) = (K_1, K_2, 0, 0)$ is globally asymptotically stable.

**Theorem 2.** Let $\tau^* = 0$. When $m_M \neq m^*$, the equilibrium $(N_1^*, N_2^*, M_1^*, M_2^*) = (K_1, K_2, 0, 0)$ is globally asymptotically stable. Thus, $(m^*, 0)$ is a global ESS. When $m_M = m^*$, then $N_i + M_i = K_i$ is an invariant set.

We use a Lyapunov function $L$, first given by Goh (1976) to prove the global asymptotic stability of a two-species Lotka-Volterra model, and an application of LaSalle’s Invariance Principle, to prove that the equilibrium $E_1$ is globally asymptotically stable. The method below follows similar steps to the analysis carried out in Lou and Wu (2011) to prove global stability in a multi-species dispersal model.

**Proposition 1** (LaSalle’s Invariance Principle). Suppose $x^*$ is an equilibrium for $\dot{x} = g(x)$ and suppose that $L$ is a weak Lyapunov function on some compact, forward-invariant neighborhood $U$ of $x^*$. Let $Z = \{x \in U : \frac{dL}{dt} = 0\}$ be the set where $L$ is not decreasing. Then, if $x^*$ is the largest
forward invariant subset of \( Z \), it is asymptotically stable and attracts every point in \( U \) (Meiss, 2007, pg. 126).

**Proof of Theorem 2.** Let

\[
L(N_1, N_2, M_1, M_2) = (N_1 - N_1^* - N_1^* \ln(N_1/K_1^*)) + (N_2 - N_2^* - N_2^* \ln(N_2/K_2^*)) + M_1 + M_2
\]

(3.15)

To apply proposition 1, we note first that the non-negative cone in \( \mathbb{R}^4 \) (i.e., \( \{ x : x \in \mathbb{R}_+^4 \} \)) contains \( E_1 = (N_1^*, N_2^*, 0, 0) \). For any given initial conditions, we can construct a compact subset of this region including the coordinate planes that is forward-invariant. Within this subset, we will show that \( \frac{dL}{dt} \leq 0 \), thus \( L \) is a weak Lyapunov function. Furthermore, \( L(N_1^*, N_2^*, 0, 0) = 0 \) (by direct substitution) and otherwise \( L(N_1, N_2, M_1, M_2) > 0 \) (this follows from the convexity of the \( \ln \) function).

Fix \( N_i^* = K_i \). Then,

\[
L(N_1, N_2, M_1, M_2) = (N_1 - K_1 - K_1 \ln(N_1/K_1^*)) + (N_2 - K_2 - K_2 \ln(N_2/K_2^*)) + M_1 + M_2
\]

(3.16)

and

\[
\frac{dL}{dt} = \frac{\dot{N}_1}{N_1}(N_1 - K_1) + \frac{\dot{N}_2}{N_2}(N_2 - K_2) + \dot{M}_1 + \dot{M}_2
\]

(3.17)

Note, from (3.6a) and (3.6b), when \( N_i^* = K_i, M_i^* = 0 \) and \( m_R = m^*, \tau_R = \tau^* \), that each of the lines in the following sum is identically zero.

\[
0 = (N_1 - N_1^*) \left[ r(1 - \frac{N_1^*}{K_1}) - d(1 - \frac{N_1^*}{N_1}) + m_R(1 - \tau_R)\tilde{K} \frac{N_2^*}{N_1^*} \right]
\]

\[
+ (N_2 - N_2^*) \left[ r(1 - \frac{N_2^*}{K_2}) + d(\frac{N_1^*}{N_2^*} - 1) - m_R(1 - \tau_R)\tilde{K} \right]
\]

\[
+ M_1 \left[ r(1 - \frac{N_1^*}{K_1}) - d(1 - \frac{N_1^*}{N_1}) + m_R(1 - \tau_R)\tilde{K} \frac{N_2^*}{N_1^*} \right]
\]

\[
+ M_2 \left[ r(1 - \frac{N_2^*}{K_2}) + d(\frac{N_1^*}{N_2^*} - 1) - m_R(1 - \tau_R)\tilde{K} \right]
\]

(3.18)
Then, from equation (3.17) we can subtract (3.18) and make the substitutions $N_i^* = K_i$, $m_R = m^*$, and $\tau_R = \tau^*$, to yield

\[
\frac{dL}{dt} = (N_1 - K_1) \left[ -\frac{r}{K_1} (N_1 - K_1 + M_1) - (d + m^*(1 - \tau^*) \tilde{K}) \left( \frac{K_2}{K_1} \frac{N_2}{N_1} \right) \right.
+ m^* \tau^* \left( \max(0, \tilde{N}) \frac{N_2}{N_1} - \max(0, -\tilde{N}) \right) \right]
+ (N_2 - K_2) \left[ -\frac{r}{K_2} (N_2 - K_2 + M_2) - d \left( \frac{K_1}{K_2} \frac{N_1}{N_2} \right) \right.
- m^* \tau^* \left( \max(0, \tilde{N}) - \max(0, -\tilde{N}) \frac{N_1}{N_2} \right) \right]
+ \left[ -\frac{r}{K_1} (N_1 - K_1 + M_1) M_1 + d(M_2 - \frac{K_2}{K_1} M_1) + m_M(1 - \tau_M) \tilde{K} M_2 
- m^*(1 - \tau^*) \tilde{K} \frac{K_2}{K_1} M_1 + m_M \tau_M (\max(0, \tilde{N}) M_2 - \max(0, -\tilde{N}) M_1) \right]
+ \left[ -\frac{r}{K_2} (N_2 - K_2 + M_2) M_2 - d \left( \frac{K_1}{K_2} M_2 - M_1 \right) - m_M(1 - \tau_M) \tilde{K} M_2 
+ m^*(1 - \tau^*) \tilde{K} M_2 - m_M \tau_M (\max(0, \tilde{N}) M_2 - \max(0, -\tilde{N}) M_1) \right] \quad (3.19)
\]

Using the following identities as in Lou and Wu (2011)

\[
\frac{K_2}{K_1} - \frac{N_2}{N_1} = \frac{N_2(N_1 - K_1) - N_1(N_2 - K_2)}{N_1 K_1} \quad (3.20a)
\frac{K_1}{K_2} - \frac{N_1}{N_2} = \frac{N_1(N_2 - K_2) - N_2(N_1 - K_1)}{N_2 K_2} \quad (3.20b)
\]

we rewrite (3.19) by setting $A = N_1 - K_1$ and $B = N_2 - K_2$. Then,

\[
\frac{dL}{dt} \left[ -\frac{r}{K_1} A^2 - \frac{r}{K_1} AM_1 - \frac{d + m^*(1 - \tau^*) \tilde{K}}{K_1} \left( \frac{N_2}{N_1} A^2 - AB \right) \right]
+ \left[ -\frac{r}{K_2} B^2 - \frac{r}{K_2} BM_2 - \frac{d}{K_2} \left( \frac{N_1}{N_2} B^2 - AB \right) \right]
+ \left[ -\frac{r}{K_1} AM_1 - \frac{r}{K_1} M_1^2 + (d + m_M(1 - \tau_M) \tilde{K}) M_2 - \frac{K_2}{K_1} (d + m^*(1 - \tau^*) \tilde{K}) M_1 \right]
+ \left[ -\frac{r}{K_2} BM_2 - \frac{r}{K_2} M_2^2 - (d \frac{K_1}{K_2} + m_M(1 - \tau_M) \tilde{K} - m^*(1 - \tau^*) \tilde{K}) M_2 + d M_1 \right]
+ m^* \tau^* \left( \max(0, \tilde{N}) \frac{N_2}{N_1} - 1 \right) - \max(0, -\tilde{N})(1 - \frac{N_1}{N_2}) \right]
+ m_M \tau_M \max(0, \tilde{N}) M_2 \quad (3.21)
\]
This can be simplified to

\[
\frac{dL}{dt} = - \left[ \frac{d + m^*(1 - \tau^*)}{K_1} \left( \frac{N_2}{N_1} A^2 - AB \right) + \frac{d}{K_2} \left( \frac{N_1}{N_2} B^2 - AB \right) \right] \\
- \frac{r}{K_1} \left[ M_1^2 + 2AM_1 + A^2 \right] \\
- \frac{r}{K_2} \left[ M_2^2 + 2BM_2 + B^2 \right] \\
+ \left[ (d + m_M(1 - \tau_M))M_2 - \frac{K_2}{K_1} (d + m^*(1 - \tau^*)\bar{K})M_1 \right] \\
+ \left[ - (d\frac{K_1}{K_2} + \bar{K}(m_M(1 - \tau_M) - m^*(1 - \tau^*)\bar{K}))M_2 + dM_1 \right] \\
+ m^*\tau^*(\frac{N_2}{N_1} - 1)(\max(0, \bar{N}) - \max(0, -\bar{N})\frac{N_1}{N_2})
\]

(3.22)

At this point, we set \( \tau^* = 0 \). By (3.5), we have the identity

\[
d + m^*\bar{K} = d\frac{K_1}{K_2}
\]

(3.23)

Then, we can simplify (3.22) to

\[
\frac{dL}{dt} = - \frac{d + m^*\bar{K}}{K_1} \left( \sqrt{\frac{N_2}{N_1} A} - \sqrt{\frac{N_1}{N_2} B} \right)^2 \\
- \frac{r}{K_1} (M_1 + A)^2 - \frac{r}{K_2} (M_2 + B)^2 \\
+ dM_2 - \frac{K_2}{K_1} (d + m^*\bar{K})M_1 \\
- (d\frac{K_1}{K_2} - m^*\bar{K})M_2 + dM_1
\]

(3.24)

(3.24a)

(3.24b)

(3.24c)

(3.24d)

The first two lines of (3.24) are clearly non-positive. The third and fourth lines sum to zero by (3.23). Therefore, \( \frac{dL}{dt} \leq 0 \) for any positive initial conditions.

Now we show that \( \frac{dL}{dt} = 0 \) either when (1) \( m_M \neq m^* \), in which case \( N_i^* = K_i \) and \( M_i^* = 0 \), or (2) \( m_M = m^* \), in which case \( N_i + M_i = K_i \). From (3.17), we see that

\[
\frac{dL}{dt} = 0 \\
\Rightarrow \dot{N}_1 (1 - \frac{K_1}{N_1}) + \dot{N}_2 (1 - \frac{K_2}{N_2}) + \dot{M}_1 + \dot{M}_2 = 0 \\
\Rightarrow \frac{K_1}{N_1} \dot{N}_1 + \frac{K_2}{N_2} \dot{N}_2 = \dot{N}_1 + \dot{N}_2 + \dot{M}_1 + \dot{M}_2 \\
\Rightarrow J(N_1, N_2) = K(N_1, N_2, M_1, M_2)
\]
where we define

\[ J(N_1, N_2) := \frac{K_1}{N_1} \dot{N}_1 + \frac{K_2}{N_2} \dot{N}_2 \] (3.25)

\[ K(N_1, N_2, M_1, M_2) := \dot{N}_1 + \dot{N}_2 + \dot{M}_1 + \dot{M}_2 \] (3.26)

Since \( m^* \tilde{K} = d\left(\frac{K_1}{K_2} - 1\right) \) by (3.5), we can simplify \( J(N_1, N_2) \) as follows:

\[ J(N_1, N_2) = K_1 \left[ r(1 - \frac{N_1 + M_1}{K_1}) - d(1 - \frac{N_2}{N_1}) + m^* \tilde{K} \frac{N_2}{N_1} \right] + K_2 \left[ r(1 - \frac{N_2 + M_2}{K_2}) + d\left(\frac{N_1}{N_2} - 1\right) - m^* \tilde{K} \right] \]

\[ = r \left[ (1 - \frac{N_1 + M_1}{K_1})K_1 + (1 - \frac{N_2 + M_2}{K_2})K_2 \right] \]

\[ - d \left[ (1 - \frac{N_2}{N_1})K_1 - (\frac{K_1}{K_2} - 1) \frac{N_2}{N_1}K_1 - (\frac{N_1}{N_2} - 1)K_2 + (\frac{K_1}{K_2} - 1)K_1 \right] \]

\[ = r \left[ (1 - \frac{N_1 + M_1}{K_1})K_1 + (1 - \frac{N_2 + M_2}{K_2})K_2 \right] - d \left[ \frac{N_1 K_2 - N_2 K_1}{N_1 K_2} \right] K_1 + d \left( \frac{N_1 K_2 - N_2 K_1}{N_2 K_2} \right) K_2 \]

\[ = r \left[ (1 - \frac{N_1 + M_1}{K_1})K_1 + (1 - \frac{N_2 + M_2}{K_2})K_2 \right] + d \left( \frac{(N_1 K_2 - N_2 K_1)^2}{N_1 N_2 K_2} \right) \]

From (3.6), we see that

\[ K(N_1, N_2, M_1, M_2) = r \left[ (1 - \frac{N_1 + M_1}{K_1})(N_1 + M_1) + (1 - \frac{N_2 + M_2}{K_2})(N_2 + M_2) \right] \]

Thus, \( J = K \) implies that

\[ r \left[ (1 - \frac{N_1 + M_1}{K_1})(N_1 + M_1 - K_1) + (1 - \frac{N_2 + M_2}{K_2})(N_2 + M_2 - K_2) \right] = d \left( \frac{(N_1 K_2 - N_2 K_1)^2}{N_1 N_2 K_2} \right) \]

\[ \Rightarrow - r \left[ \frac{(N_1 + M_1 - K_1)^2}{K_1} + \frac{(N_2 + M_2 - K_2)^2}{K_2} \right] = d \left( \frac{(N_1 K_2 - N_2 K_1)^2}{N_1 N_2 K_2} \right) \]

(3.27)

Since \( r, d, K_i > 0 \), the left- and right-hand sides of (3.27) must be identically zero, so we see that

\[ N_i + M_i = K_i, \quad \text{and} \]

\[ N_1 = \frac{K_1}{K_2} N_2. \] (3.28a)

(3.28b)

From (3.28a) and (3.28b), we see that either

\[ M_i = 0, \quad \text{or} \]

\[ \frac{M_1}{M_2} = \frac{K_1}{K_2}. \] (3.29a)

(3.29b)
By plugging (3.28a) and (3.28b) into (3.6a) and (3.6b), one can easily show that $\dot{N}_1 = 0$ and $\dot{N}_2 = 0$. Plugging (3.28a) into (3.6c) and (3.6d), we see that $M_2(d + m_M \tilde{K}) = dM_1$. Therefore, either (3.29a) holds, so $M_i = 0$, or (3.29b) holds from which it follows that $m_M = d\left(1 + \frac{K_1}{K_2}\right)$. Thus, $m_M = m^*$ by (3.5).

In sum, when $m_M \neq m^*$, $\frac{dL}{dt} = 0$ only when $N_i^* = K_i, M_i^* = 0$ which proves that $(m^*, 0)$ is a global ESS. Note that if $m_M = m^*$, then the manifold given by $N_i + M_i = K_i$ is invariant. \qed

When $\tau^* \neq 0$ and $m_R \neq m^*$, we cannot solve explicitly for the values $(N_1^*, N_2^*)$. Nevertheless, by applying tools from adaptive dynamics (e.g., Metz et al., 1996; Geritz et al., 1998; Kisdi and Geritz, 2010), we can show that $(m^*, \tau^*)$ is locally convergence stable. Before stating and proving this result, we introduce some necessary lemmas (proofs in appendix D), and then we formalize the assumption made in the introduction. For each lemma, we assume that $(N_1, N_2, M_1, M_2) = (N_1^*, N_2^*, 0, 0)$.

**Lemma 2.** Let $\lambda^{(1)}$ and $\lambda^{(2)}$ represent the eigenvalues of $J_2$. Then, when $(m_R, \tau_R) = (m_M, \tau_M)$, $\lambda^{(1)} = 0$ and $\lambda^{(2)} < 0$.

**Lemma 3.** When $\tilde{N} > 0$, it follows that $N_2^* > K_2$ and $N_1^* < K_1$. Similarly, when $\tilde{N} < 0$, it follows that $N_2^* < K_2$ and $N_1^* > K_1$.

**Lemma 4.** Fix $\tau_R = \tau^*$. Then, $m^*$ is uniquely determined by (3.5). When $m_R < m^*$, $\tilde{N} > 0$. Similarly, when $m_R > m^*$, $\tilde{N} < 0$.

**Lemma 5.** Fix $\tau = \tau^*$. Then, $m^*$ is uniquely determined by (3.5). Let $m_R = m_M = m$ and $\tau_R = \tau_M = \tau^*$. Denote the largest eigenvalue of $J_2$ by $\lambda^{(1)}$. Then, $\frac{\partial\lambda^{(1)}}{\partial m_M} > 0$ when $m < m^*$, and $\frac{\partial\lambda^{(1)}}{\partial m_M} < 0$ when $m > m^*$.

**Lemma 6.** Fix $m_R = m_M = m^*$. Then $\tau^*$ is uniquely determined by (3.5). Let $\tau_R = \tau_M = \tau$. Then, $\frac{\partial\lambda^{(1)}}{\partial \tau_M} > 0$ when $\tau < \tau^*$, and $\frac{\partial\lambda^{(1)}}{\partial \tau_M} < 0$ when $\tau > \tau^*$.

**Conjecture 1.** Consider a resident population at equilibrium. If a mutant can increase when rare
and if the resident would be unable to increase when rare when the mutant is at equilibrium, then the mutant displaces the resident.

**Theorem 3.** Consider the system of equations given by (3.6). Then, \((m^*, \tau^*)\) is a continuously stable strategy (CSS).

**Proof.** Recall that the mutant growth rate when rare is given by the dominant eigenvalue, \(\lambda^{(1)}\), of the Jacobian matrix (3.14) evaluated at \((N_1^*, N_2^*, 0, 0)\). When \((m, \tau) = (m^*, \tau^*)\) for both the resident and the mutant, then at the equilibrium, \(N_i^* = K_i\), \(M_i^* = 0\), and we see that \(\tilde{N} = 0\). Also, for these parameter values, \(\lambda^{(1)} = 0\) and \(\lambda^{(2)} < 0\), by lemma 2. It can be shown that the optimal strategy (3.5) can be derived by setting the partial derivatives of \(\lambda^{(1)}\) (i.e., the selection gradient, Marrow et al. (1992)) with respect to \(m_M\) (i.e., \(\frac{\partial \lambda^{(1)} (i)}{\partial m_M}\)) and also \(\tau_M\) (i.e., \(\frac{\partial \lambda^{(1)} (i)}{\partial \tau_M}\)) equal to zero. Thus, by construction \((m^*, \tau^*)\) is an evolutionarily singular strategy (Geritz et al., 1997, 1998). Away from \((m^*, \tau^*)\), the partial derivatives will be non-zero and the signs of these derivatives indicate the direction of selective pressure on these traits (Hastings, 1983, his appendix).

To visualize how a trait substitution sequence (Metz et al., 1992; Dieckmann and Law, 1996) might develop, consider the coordinate plane in parameter space given by \(m\) and \(\tau\). Equation (3.5) defines a curve in this space, the ESSet (figure 3.3), along which, \((N_1^*, N_2^*) = (K_1, K_2)\). This curve separates the \(m - \tau\) plane into two regions. We see from lemmas 3 and 4 that above this curve (region I), \(N_1^* > K_1\), \(N_2^* < K_2\), and \(\tilde{N} < 0\), whereas below this curve (region II), the inequalities are reversed. Consider a resident playing a strategy in region I. By lemmas 5 and 6, a mutant with a lower value of \(m_M\) and/or a higher value of \(\tau_M\) than the resident will be able to increase when rare. By conjecture 1, the mutant will be able to invade and replace the resident, thus becoming in effect the new resident. Notice that in Euclidean distance, the mutant’s strategy is closer to the ESSet than is the resident’s strategy. A similar result applies if the resident is playing a strategy in region II. Therefore, \((m^*, \tau^*)\) is convergence stable. We conclude that \((m^*, \tau^*)\) is an ESS since selection pressures prevent a mutant playing a strategy different from \((m^*, \tau^*)\) to increase when rare. Since \((m^*, \tau^*)\) is both an ESS and convergence stable, it is a CSS.
3.5 Travel costs

In this section, we find an optimal strategy, denoted \((m^{**}, 0)\), when travel costs are considered (i.e., \(k > 0\)). We only consider when organisms use resource information to guide conditional movements (i.e., \(\tau = 0\)) so that we can analytically solve for \(m^{**}\). This optimal strategy differs fundamentally from the previous \(m^*\) strategy (i.e., equation (3.5)) in that a resident subject to travel costs playing \(m^{**}\) will not be distributed at the ideal free distribution. Rather, if the travel cost is not too great, the resident’s equilibrium abundance equals the carrying capacity of the smaller patch but not of the larger patch (i.e., \(N_1^* < K_1, N_2^* = K_2\)). Simulations show that when \(\tau \neq 0\), strategies that lead to \(N_2^* = K_2\) (and \(N_1^* < K_1\)) are evolutionarily stable, but this is biologically irrelevant for the following reason. \(\tilde{N}\) as previously defined is a correct measure of the relative fitness differential between patches when there are no travel costs. But, in the presence of travel costs, organisms ought to include these costs in their calculation of fitness differences (Rosenzweig, 1981; Morris, 1987).

We show when the resident plays \((m^{**}, 0)\) that the equilibrium is globally asymptotically stable, and we prove that this optimal strategy is convergence stable. Consider equations (3.6)
when $\tau = 0$, namely

$$
\dot{N}_1 = g(N_1, M_1; K_1) \cdot N_1 - dN_1 + (1 - k)(d + m_R \tilde{K})N_2 
$$  (3.30a)

$$
\dot{N}_2 = g(N_2, M_2; K_2) \cdot N_2 + (1 - k)dN_1 - (d + m_R \tilde{K})N_2 
$$  (3.30b)

$$
\dot{M}_1 = g(M_1, N_1; K_1) \cdot M_1 - dM_1 + (1 - k)(d + m_M \tilde{K})M_2 
$$  (3.30c)

$$
\dot{M}_2 = g(M_2, N_2; K_2) \cdot M_2 + (1 - k)dM_1 - (d + m_M \tilde{K})M_2 
$$  (3.30d)

**Theorem 4.** When $m_R = m_M = m$, the Jacobian of (3.30) evaluated at $(N_1^*, N_2^*, 0, 0)$ has zero determinant.

**Proof.** Direct calculation of the Jacobian matrix of the invasion matrix of (3.30) (i.e., $J_2$ as in section 3.4) yields

$$
J_2 = \begin{bmatrix}
    r(1 - \frac{N_1^*}{K_1}) - d & (d + m_M \tilde{K})(1 - k) \\
    d(1 - k) & r(1 - \frac{N_2^*}{K_2}) - (d + m_M \tilde{K})
\end{bmatrix}
$$

Setting equations (3.30a) and (3.30b) in turn equal to zero, we can rearrange terms to show that at the equilibrium, the following must hold (note that we neglect the trivial case $(N_1^*, N_2^*) = (0, 0)$):

$$
d + m_R \tilde{K} = \frac{N_1^*}{N_2^*} \left( \frac{d}{1 - k} - \frac{r}{1 - k}(1 - \frac{N_1^*}{K_1}) \right) 
$$  (3.31a)

$$
d + m_R \tilde{K} = d(1 - k) \frac{N_1^*}{N_2^*} + r(1 - \frac{N_2^*}{K_2}) 
$$  (3.31b)

The determinant of $J_2$, is:

$$
|J_2| = A - B
$$

where

$$
A = r^2(1 - \frac{N_1^*}{K_1})(1 - \frac{N_2^*}{K_2}) - dr(1 - \frac{N_2^*}{K_2}) - r(1 - \frac{N_1^*}{K_1})(d + m_M \tilde{K}) + d(d + m_M \tilde{K})
$$

and

$$
B = d(d + m_M \tilde{K})(1 - k)^2.
$$
Letting \( m = m_R = m_M \), we see that by (3.31b),
\[
A = r^2(1 - \frac{N_1^*}{K_1})(1 - \frac{N_2^*}{K_2}) - dr(1 - \frac{N_2^*}{K_2}) - r(1 - \frac{N_1^*}{K_1})\left(d(1-k)\frac{N_1^*}{N_2^*} + r(1 - \frac{N_2^*}{K_2})\right)
\]
\[+ d(d(1-k))\frac{N_1^*}{N_2^*} + r(1 - \frac{N_2^*}{K_2})\right)
\]
\[= d(1 - k)\frac{N_1^*}{N_2^*}(d - r(1 - \frac{N_1^*}{K_1}))
\]
(3.32)

By (3.31a),
\[
B = d(d + m\tilde{K})(1 - k)^2
\]
\[= d\frac{N_1^*}{N_2^*}\left(\frac{d}{1-k} - \frac{r}{1-k}(1 - \frac{N_1^*}{K_1})\right)(1 - k)^2
\]
(3.34)
\[= d(1 - k)\frac{N_1^*}{N_2^*}(d - r(1 - \frac{N_1^*}{K_1}))
\]
(3.35)

Therefore, \(|J_2| = A - B = 0\).

When the trace of \( J_2 \) is negative, \( \lambda^{(1)} = 0 \) is the dominant eigenvalue. Then, as in section 3.4, this eigenvalue is the linearized growth rate of a mutant when rare. We wish to find the value of \( m^{**} \) such that \( \lambda^{(1)} \big|_{m_R=m_{**}} \) is a maximum when \( m_R = m_M = m^{**} \). Necessary and sufficient conditions are that \( \frac{\partial \lambda^{(1)}}{\partial m_R} = 0 \) and \( \frac{\partial^2 \lambda^{(1)}}{\partial m_R^2} + \frac{\partial^2 \lambda^{(1)}}{\partial m_M^2} < 0 \) (Maynard Smith, 1982; Geritz et al., 1998; Diekmann, 2004). By observation, \( \frac{\partial^2 \lambda^{(1)}}{\partial m_M^2} = 0 \). We will need the following preliminary result to establish that \( m^{**} \) is an ESS.

**Lemma 7.** Assume \( d < r \). \( \frac{\partial N_1^*}{\partial m_R} > 0 \) when evaluated at the optimal strategy \( m^{**} \).

**Proof.** Without loss of generality, let \( r = 1 \). Then, by equations (3.30a) and (3.30b),
\[
F(N_1^*, N_2^*) := \dot{N}_1|_{N_1^*, N_2^*} = 0
\]
\[= g(N_1^*, 0; K_1) \cdot N_1^* - dN_1^* + (1 - k)(d + m_R\tilde{K})N_2^*
\]
\[= \left(1 - \frac{N_1^*}{K_1}\right)N_1^* - dN_1^* + (1 - k)(d + m_R\tilde{K})N_2^*
\]

Taking the derivative of \( F \) with respect to \( m_R \), evaluating \( N_1^*, N_2^* \), and \( m_R \) at \( m = m^{**} \) as given in (3.38), (3.39), and (3.40), and solving for \( \frac{\partial N_1^*}{\partial m_R} \) and simplifying, we have
\[
\frac{\partial N_1^*}{\partial m_R} = \frac{(1 - k)K_2^2\tilde{K}}{d(1-k)(1 + dk(-2 + k))K_1 + (2d(k - 1)^2 + (1 - d))K_2}
\]
Therefore, as long as \( d < 1 \),
\[
\frac{\partial N_1^*}{\partial m_R} |_{m_R = m^{**}} > 0
\]

This leads to the following result.

**Theorem 5.** The strategy \((m^{**}, 0)\) given by
\[
m^{**} = \left( (1 - k)(r - d + d(1 - k)^2) \frac{K_1}{rK_2} - 1 \right) \frac{d}{K}
\]
is a CSS when this is non-negative. A resident playing \( m^{**} \geq 0 \) has an equilibrium abundance
\[
(N_1^*, N_2^*) = (K_1(1 - \frac{d}{r}(1 - (1 - k)^2)), K_2).
\]

**Proof.** Since \( \frac{\partial \lambda^{(1)}}{\partial m_M} |_{m_M = m_R = m^{**}} = 0 \) and \( \lambda^{(1)} |_{m_M = m_R} = 0 \), and because the determinant of \( J_2 \) is the product of its eigenvalues, we see that
\[
\frac{\partial |J_2|}{\partial m_M} |_{m_M = m_R = m^{**}} = \frac{\partial}{\partial m_M} [\lambda^{(1)} \cdot \lambda^{(2)}] |_{m_M = m_R = m^{**}}
\]
\[
= [\lambda^{(2)} \frac{\partial \lambda^{(1)}}{\partial m_M} + \lambda^{(1)} \frac{\partial \lambda^{(2)}}{\partial m_M}] |_{m_M = m_R = m^{**}}
\]
\[
= 0 \quad (3.36)
\]
But, by direct calculation,
\[
\frac{\partial |J_2|}{\partial m_M} = -r(1 - \frac{N_1^*}{K_1})\tilde{K} + d\tilde{K} - d\tilde{K}(1 - k)^2
\]
\[
(3.37)
\]
Therefore,
\[
N_1^* = K_1(1 - \frac{d}{r}(1 - (1 - k)^2)) \quad (3.38)
\]
Plugging (3.38) into (3.30a) yields
\[
N_2^* = \frac{d(1 - k)K_1(K_1 + K_2)(r - d(1 - (1 - k)^2))}{(d(K_1 + K_2) + (K_1 - K_2)m^{**})r} \quad (3.39)
\]
Then, plugging (3.39) into (3.30b) yields

\[ m^{**} = \left( (1 - k)(r - d + d(1 - k)^2) \frac{K_1}{rK_2} - 1 \right) \frac{d}{K} \]  

(3.40)

Finally, using equation (3.40), (3.39) simplifies to \( N^*_2 = K_2 \).

Notice that

\[ \frac{\partial^2 |J_2|}{\partial m_M \partial m_R} = \frac{\partial}{\partial m_R} \left[ -r(1 - N^*_1 K_1 \hat{K} + d \hat{K} - d(1 - k)^2) \right] \]

\[ = \frac{r}{K_1^2} \hat{K} \frac{\partial N^*_1}{\partial m_R} \]

Since \( \lambda^{(1)} = 0 \) and \( \lambda^{(2)} < 0 \) when \( m_M = m_R \), and \( \frac{\partial \lambda^{(1)}}{\partial m_M} = \frac{\partial \lambda^{(1)}}{\partial m_R} = 0 \) when \( m_M = m_R = m^{**} \), we have that

\[ \frac{\partial^2 |J_2|}{\partial m_M \partial m_R} = \lambda^{(2)} \frac{\partial^2 \lambda^{(1)}}{\partial m_M \partial m_R} \]

when evaluated at \( m_M = m_R = m^{**} \). Thus, we need \( \frac{\partial^2 |J_2|}{\partial m_M \partial m_R} > 0 \) for \( \frac{\partial^2 \lambda^{(1)}}{\partial m_M \partial m_R} < 0 \). An application of lemma 7 gets us this result.

When (3.40) is negative, it is unclear if \( m^{**} = 0 \) is convergence stable. We can calculate the selection gradient \( \frac{\partial \lambda^{(1)}}{\partial m_M} \big|_{m_M=m_R=0} \) from \( \frac{\partial}{\partial m_M} |J_2| \big|_{m_M=m_R=0} \) and, after using equation (3.30a),

\[ \frac{\partial}{\partial m_M} |J_2| \big|_{m_M=m_R=0} = \hat{K} (1 - k) d \left( \frac{N^*_2}{N^*_1} - (1 - k) \right) \]  

(3.41)

Since \( \frac{\partial}{\partial m_M} |J_2| \big|_{m_M=m_R=0} = \left[ \lambda^{(2)} \frac{\partial \lambda^{(1)}}{\partial m_M} + \lambda^{(1)} \frac{\partial \lambda^{(2)}}{\partial m_M} \right] \big|_{m_M=m_R=0} \) and \( \lambda_1 |_{m_M=m_R=0} = 0 \) by theorem 4, we can show that selection will be for smaller values of \( m \) (i.e., \( \frac{\partial \lambda^{(1)}}{\partial m_M} < 0 \)) when \( m = 0 \) if we can show that \( \lambda^{(2)} < 0 \) and \( \frac{\partial}{\partial m_M} |J_2| \big|_{m_M=m_R=0} > 0 \). In general, this cannot be shown, although if we assume that \( r > 3d \), then \( m^{**} \) is guaranteed to be convergence stable (theorem 6).

**Theorem 6.** Let \( m^{**} \) and \( \frac{\partial}{\partial m_M} |J_2| \big|_{m_M=m_R=0} \) be as given in (3.40) and (3.41) respectively. Assume that \( r > 3d \). Then, when \( m^{**} < 0 \), the strategy \( m = 0 \) is convergence stable.

**Proof.** We must show that

\[ \lambda^{(2)} < 0, \quad \text{and} \]

\[ \frac{\partial}{\partial m_M} |J_2| \big|_{m_M=m_R=0} > 0 \]  

(3.42a)

(3.42b)
when $m^{**} < 0$. To do this, we first establish the following preliminary facts:

(1) there exists a $\hat{k}$ such that $m^{**} = 0$

(2) $\frac{\partial N^*_i}{\partial k} < 0$

From these two preliminary facts, we will be able to prove (3.42).

To establish (1), first notice that $m^{**} = m^* > 0$ when $k = 0$ (where $m^*$ is given by (3.5) in section 3.2). Also, $m^{**} = -\frac{d}{K} < 0$ when $k = 1$.

$$\frac{\partial m^{**}}{\partial k} = -\frac{d}{K} \left[ (r - d + d(1-k)^2) + 2d(1-k)^2 \right] \frac{K_1}{rK_2}$$

$$< 0, \text{ for all } k \leq 1$$

since $r > d$ by assumption. Therefore, $m^{**}$ is strictly decreasing on $k \in [0, 1]$. Since $m^{**}$ is a continuous function of $k$, the Intermediate Value Theorem guarantees there exists a value of $k = \hat{k}$ such that $m^{**} = 0$ when $k = \hat{k}$.

Now, we establish (2). At equilibrium, when $m_R = 0$, we see from (3.30a) and (3.30b) that

$$\frac{N^*_2}{N^*_1} = \frac{d - r(1 - N^*_1 K_1)}{d(1-k)} \quad (3.43a)$$

$$\frac{N^*_1}{N^*_2} = \frac{d(1-k)}{d - r(1 - N^*_2 K_2)} \quad (3.43b)$$

Equating (3.43a) and (3.43b) yields

$$[d(1-k)]^2 = [d - r(1 - \frac{N^*_1}{K_1})][d - r(1 - \frac{N^*_2}{K_2})] \quad (3.44)$$

Taking the partial derivative of (3.44) with respect to $k$ and applying (3.43) yields

$$-2d^2(1-k) = \left[ \frac{r}{K_1} \frac{\partial N^*_1}{\partial k} \left( d - r(1 - \frac{N^*_2}{K_2}) \right) + \frac{r}{K_2} \frac{\partial N^*_2}{\partial k} \left( d - r(1 - \frac{N^*_1}{K_1}) \right) \right]$$

$$= \frac{r}{K_1} \frac{\partial N^*_1}{\partial k} \left( d(1-k) \frac{N^*_1}{N^*_2} \right) + \frac{r}{K_2} \frac{\partial N^*_2}{\partial k} \left( d(1-k) \frac{N^*_2}{N^*_1} \right)$$

$$\implies -2d = r \left[ \frac{\partial N^*_1}{\partial k} \frac{N^*_1}{K_1 N^*_2} + \frac{\partial N^*_2}{\partial k} \frac{N^*_2}{K_2 N^*_1} \right] \quad (3.45)$$
We can rewrite (3.45) as

\[ 0 = \left[ \frac{r}{K_1} \frac{\partial N_1^*}{\partial k} \right] N_1^* + \left[ \frac{r}{K_2} \frac{\partial N_2^*}{\partial k} \right] N_2^* + 2d \]  

(3.46)

Then, (3.46) is of the elementary form \( ax + bx + c = 0 \) which can be solved for \( x \) and \( \frac{1}{x} \) by multiplying through by \( x \) and applying the quadratic formula. Doing so for (3.46) yields

\[ \frac{N_2^*}{N_1^*} = -d \pm \sqrt{d^2 - \frac{r^2}{K_1 K_2} \frac{\partial N_2^*}{\partial k} \frac{\partial N_1^*}{\partial k} K_2} \]  

(3.47)

We know that \( \frac{N_2^*}{N_1^*} \) is real, so the discriminant must be positive. Furthermore, both \( \frac{N_2^*}{N_1^*} \) and \( \frac{N_2^*}{N_2^*} \) are positive which implies that \( \frac{\partial N_2^*}{\partial k} < 0 \). Using the quadratic formula to solve (3.46) for \( \frac{N_2^*}{N_1^*} \) yields that \( \frac{\partial N_2^*}{\partial k} < 0 \).

Now that we have established (1) and (2), we use these to prove (3.42). First, we show that \( \lambda(2) < 0 \) when \( m_R = m_M = 0 \) and \( 1 > k > \hat{k} \). When \( m_M = m_R = 0 \), it follows that \( |J_2| = 0 \) and \( tr(J_2) = r(1 - \frac{N_1^*}{K_1}) - d + r(1 - \frac{N_2^*}{K_2}) - d \) by theorem 4. When \( m = m^{**} \), \( tr(J_2) < 0 \) by theorem 5. Since \( \frac{\partial N_2^*}{\partial k} < 0 \), it might be that \( tr(J_2) > 0 \) as \( k \to 1 \). But, we see from (3.30a) and (3.30b) that

\[ N_i^* = K_i \left( 1 - \frac{d}{r} \right) \]  

(3.48)

when \( k = 1 \). Plugging these equilibrium values into \( tr(J_2) \), we find that \( tr(J_2) = 0 \) when \( k = 1 \), thus since \( \frac{\partial N_i^*}{\partial k} < 0 \), \( tr(J_2) < 0 \) for all \( k < 1 \). Since \( tr(J_2) = \lambda(1) + \lambda(2) \), but \( \lambda(1) = 0 \) when \( m_R = m_M \), we see that \( \lambda(2) < 0 \).

Now, when \( m^{**} = 0 \), \( \frac{\partial}{\partial m_M} |J_2|_{m_M=m_R=0} = 0 \). By showing that

\[ \frac{\partial}{\partial k} \left( \frac{\partial}{\partial m_M} |J_2|_{m_M=m_R=0} \right) = 1 + \frac{N_1^* \frac{\partial N_2^*}{\partial k} - N_2^* \frac{\partial N_1^*}{\partial k}}{(N_1^*)^2} > 0 \]  

(3.49)

we can establish that \( \frac{\partial}{\partial m_M} |J_2|_{m_M=m_R=0} > 0 \) when \( m^{**} < 0 \). Note that we can solve (3.46) for \( \frac{\partial N_2^*}{\partial k} \) and rearrange (3.49) to yield

\[ \frac{\partial N_2^*}{\partial k} = \left[ \frac{2d N_1^* K_2}{r} \right] - \frac{\partial N_1^*}{\partial k} \left( \frac{N_1^*}{N_2^*} \right)^2 K_2 \]  

(3.50a)

\[ N_2^* \frac{\partial N_1^*}{\partial k} - \frac{2d N_1^* K_2}{r} < (N_1^*)^2 \]  

(3.50b)
Plugging (3.50a) into (3.50b) and simplifying, we find that (3.49) will be satisfied if
\[
\frac{\partial N_1^*}{\partial k} < \frac{N_1^*(1 - \frac{2dK_2}{rN_2^*})}{K_2\left(\frac{N_1^*}{N_2^*}\right)^2 + \frac{N_2^*}{N_1^*}}
\] (3.51)

Since we already established that \(\frac{\partial N_1^*}{\partial k} < 0\), we see that (3.51) will certainly hold if \(N_2^* > \frac{2d}{r}K_2\).

The minimum of \(N_2^*\) is \(N_2^* = K_2(1 - \frac{d}{r})\) by (3.48). Thus, \(N_2^* > \frac{2d}{r}K_2\) will obviously hold when \(K_2(1 - \frac{d}{r}) > \frac{2d}{r}K_2\) which is true when \(r > 3d\). Therefore, \(r > 3d\) is a sufficient condition for (3.51) and (3.49) and thus for \(\frac{\partial}{\partial m_M} |J_2||_{m_M=m_R=0} > 0\) to hold.

\[\square\]

3.6 Discussion

Previous mathematical analyses of general single-species, discrete space, continuous time dispersal models have been successful in proving the global stability of a positive equilibrium point when per capita movement rates are either fixed or depend on conditions in a single patch (Freedman and Waltman, 1977; Holt, 1985; Freedman et al., 1986), see Goh (1977); Lou and Wu (2011) for multi-species stability. It appears to be more difficult to prove existence, feasibility, or uniqueness of an equilibrium since this has been assumed in many results of global asymptotic stability for general systems (e.g., Goh, 1977; Hastings, 1978a,b; Freedman et al., 1986). Here, we have been partially successful in proving the global asymptotic stability of a single-species, two-patch system that includes travel costs with the additional non-linearities introduced by fitness-based movement.

We were also able to show that the optimal strategy \((m^*, \tau^*)\) is a CSS. It has been noted previously in systems where organisms’ instantaneous fitness is zero at equilibrium and there are no costs to movement that linear stability analysis is insufficient to conclude whether a mutant will be able to increase when rare. In these types of model systems, the growth rate of a mutant equals the growth rate of the resident at equilibrium which, by virtue of the system being at equilibrium, must also equal zero. Also, if the mutant’s growth rate when rare is a linear function of the mutant’s strategy, then this leads to a degenerate case of an ESS (Geritz et al., 1998). However, if the model is tractable so that computer algebra systems will yield eigenvalues and eigenvectors, then a center
manifold reduction can tell us if a movement strategy is a local ESS. We found this technique effective only when $\tau = 0$. It is interesting to note that an approach using Lyapunov functions was successful in proving that the optimal strategy is a global ESS. Furthermore, using basic tools from linear algebra and dynamical systems theory, we were able to show that the optimal strategy is convergence stable. Specifically, we were able to show that variants using strategies closer to optimal (as measured by Euclidean distance) can increase when rare when competing against a resident species. We tried applying the convergence stability criteria (2.4) and (2.5) from chapter 2, but the second criteria (2.5) fails to hold (see appendix D and theorem 7). The reason for this is that the direction of the eigenvector corresponding to the zero eigenvalue of the Jacobian matrix is tangent to the ESSet (3.5). In other words, multiplying the matrix by the vector $[m^*, 1-\tau^*]^T$ (i.e., the slope of the ESSet), returns the zero vector. This means that a second strategy that differs infinitesimally from a given optimal strategy will be equivalently optimal if the second strategy’s deviation from the first is in the direction of the tangent to the ESSet. This confirms what we saw in chapter 2, that any strategy along the ESSet offers equal fitness. Thus, the strategy $(m^*, \tau^*)$ is neutrally stable with respect to any other strategy in the ESSet.

Our results on population distributions in systems with travel costs are consistent with previous results (e.g., Kennedy and Gray, 1997; Matsumura et al., 2010; DeAngelis et al., 2011), that is, abundances become more similar when travel costs are included. It is interesting to note that the effects of travel costs for optimally moving organisms constrained by perceptual limitations are apparent only in one patch, since $N_2^* = K_2$ both with and without these costs. The reason for this is unclear at this point, but this prediction may be worth exploring in experimental systems where population dynamics are considered in tandem with travel costs.

Optimal information use in the presence of travel costs results in a fitness gradient between patches at equilibrium because the instantaneous per capita fitness of the consumer is zero in the second patch whereas the fitness in the first patch is positive. This agrees with Rosenzweig (1981, pg. 330) who concluded that “habitat selection should be abandoned even before density is high enough to equalize fitness in the two patches.” DeAngelis et al. (2011) and Lou and Wu (2011)
studied optimal movement in a bi-trophic (and also tri-trophic) patch model with travel costs. In their models, the consumer species was forced to emigrate from one patch at a constant rate due to environmental effects (e.g., stream flow) but the other species were sessile. For their two-patch model, they also found that per capita instantaneous fitness of the consumer species remains zero in the downstream patch. Furthermore, the fitness in their upstream patch increases by (in our notation) $d(1 - (1 - k)^2)$. We find identical results in our model, namely that per capita fitness in patch 1 is increased from 0 to $r(1 - \frac{N_1^*}{K_1}) = d(1 - (1 - k)^2)$ when travel costs are included. This is related to the idea of “balanced dispersal” (cf. McPeek and Holt (1992)) in a two-patch system with an asymptotically stable equilibrium. Balanced dispersal, in the context of a single species with density-dependent growth limited by a patch-specific carrying capacity, implies that the ratio given by dispersal rates from one patch divided by dispersal rates from another patch will be inversely proportional to the ratio of the carrying capacities of the two patches (McPeek and Holt, 1992). This follows directly when instantaneous fitness equals zero in every patch. For a single-species model with a globally stable positive equilibrium, balanced dispersal leads to an ideal free distribution. For example, in our single-species model (3.3), this ratio is $\frac{d}{d(K_1/K_2)} = \frac{K_2}{K_1} = \frac{N_2^*}{N_1^*}$. Thus, in the absence of costs, optimally dispersing organisms will equilibrate at full carrying capacity (i.e., $N_i^* = K_i$).

In the presence of travel costs, when organisms are acting optimally (i.e., $m = m^{**} \geq 0$), we see that $N_2^* = K_2$, so fitness is zero in the second patch. Thus, net dispersal into patch two is also zero at equilibrium, and we see that this ratio of dispersal rates (discounting the cost of emigrating) is $\frac{d(1-k)}{d+m^{**}K} = \frac{K_2}{K_1(1-\frac{2}{d}(1-(1-k)^2))} = \frac{N_2^*}{N_1^*}$. Dispersal is clearly not balanced when travel costs are included, however the ratio of the effective dispersal rates in the presence of optimal movement remains equal to the ratio of the patch equilibria. This assumes that $m^{**} \geq 0$. For large $k$, the value of $m^{**}$ given by (3.40) is negative. In this case, $m = 0$ is the best strategy. Therefore, we reason that beyond a certain threshold of costs, organisms should not use any available information to guide movement.

In conclusion, we have extended previous mathematical work on the ecological and evolutionary stability analysis of movement strategies for single-species, two-patch systems by including both fitness and resource information into a conditional movement strategy. Through our analysis of
systems with and without costs, we have demonstrated how one might identify optimal movement strategies when non-linear population dynamics and movement occur at the same trophic level. Finally, we showed that an adaptive strategy for organisms subject to travel costs and perceptual constraints does not lead to an ideal free distribution and suggested testable theoretic predictions for future empirical research.
4.1 Introduction

Difference equations are used to model population abundances and dispersal when births and dispersal are periodic. The single-species equations in the absence of stage structure (i.e., different age classes) take the form of a one-dimensional map, \( x' = f(x; r, \alpha) \). \( x \) represents population abundance, \( ' \) denotes the next generation, \( r \) is the density-independent growth rate, and \( \alpha \) represents other model parameters. Common one-dimensional growth equations include the logistic, \( f(x) = r x (1 - x) \); the Ricker, \( f(x) = x \exp(r(1 - \frac{x}{K})) \); the Hassell, \( f(x) = \frac{rx}{1+ax} \); and the generalized Beverton-Holt, \( f(x) = \frac{rx}{1+(x/K)^\gamma} \) (Ricker, 1954; Beverton and Holt, 1957; Hassell, 1975; May, 1976, 1977; Geritz and Kisdi, 2004). The maps have the common property that increasing \( r \) often leads to increased dynamical complexity, sometimes to chaotic dynamics. Two-species models, predator-prey or host-parasitoid, can be assembled as extensions of these single-species models (Nicholson, 1933; Edelstein-Keshset, 2005).

Recently, there has been interest in studying spatial extensions of these models where a single species of organisms exists in a patchy environment (Hassell et al., 1991; Allen et al., 1993; Hastings, 1993; Gyllenberg et al., 1993; Doebeli, 1995). Two main modeling approaches have emerged. The first approach is to couple together two (or more) patches where the dynamics in one patch can
influence the dynamics in the others, e.g.,

\[ x'_1 = x_1 f_1(x_1) - d_1 x_1 + d_2 x_2 \]  
\[ x'_2 = x_2 f_2(x_2) + d_1 x_1 - d_2 x_2 \] (4.1a) (4.1b)

where per capita population growth in each patch is given by \( f_i(x_i) \) (Hastings, 1993). The second approach is to study the single-patch dynamics as a function of immigration from an unspecified outside source, e.g.,

\[ x' = x f(x) + c = F(x) \] (4.2)

where \( c \) represents the abundance of immigrants (McCallum, 1992). The aim of the two-patch studies has been to discover exactly how patchiness affects the entire population dynamics of the environment. Various authors using the first approach (4.1) have described the dynamics of population growth with symmetric (Hastings, 1993; Gyllenberg et al., 1993) and asymmetric unconditional dispersal (Doebeli, 1995). For symmetric dispersal rates, when the single-patch population dynamics are chaotic, small dispersal rates can lead to two types of period-two solutions. The value of \( r \) and the initial conditions play a role in which solution is observed. The first type is an in-phase solution with both patches oscillating in phase, and the second is an anti-phase solution with the total population abundance being constant over time (Hastings, 1993). Thus, dispersal can stabilize the overall dynamics. Asymmetric dispersal rates are even more likely to lead to stable system dynamics (Doebeli, 1995).

With the second approach (4.2), Stone (1993) and Stone and Hart (1999) showed that immigration into a patch with otherwise chaotic population dynamics can stabilize the dynamics through a series of period-halving bifurcations that ultimately result in a stable equilibrium point, though this result is model-dependent. As might be expected, excessive emigration or harvesting from a patch can destabilize the dynamics leading to extinction (but see Sinha and Parthasarthy, 1996, for a counter-example).

Dispersal has been shown to evolve from many different underlying population models as well as varying dynamical regimes (Comins et al., 1980; Hamilton and May, 1977; Holt and McPeek,
1996; McPeek and Holt, 1992). A necessary condition for this trait to evolve is: a dispersing organism must have a higher reproductive rate when rare relative to similar non-dispersing organisms in the given ecological environment. This is also sufficient when an ecological model has a single dynamical attractor. When there are multiple attractors, the effects of population dynamics over time and space can change the dynamics of the ecological environment. In this case, small changes in quantitative traits can lead to attractor switching (Geritz et al., 2002). For example, the evolution of dispersal can change the initial attractor of the ecological dynamics, sometimes to the detriment of the disperser. If the new ecological environment is unfavorable to the disperser whose presence created these dynamics, then it is possible that even though the disperser was able to increase when rare under one dynamical regime, it is no longer able to do so under the new dynamical regime, essentially because the fitness landscape has changed. This can cause the disperser to go extinct (Doebeli, 1998).

More generally, evolutionary branching may occur (Geritz et al., 1997, 1998) if, due to frequency dependence, a trait evolves to a minimum of the fitness landscape. At this point there may be disruptive selection where the single quantitative trait diverges at the branching point becoming two different quantitative traits, one more positive, the other more negative, than the original trait (Geritz et al., 1997, 1998; Dieckman and Doebeli, 1999). Thus, at this minimum point on the fitness landscape, different values of the trait may be selected for. This phenomenon has been well documented by theoretical studies using the tools of adaptive dynamics and evolutionary game theory (Metz et al., 1992; Marrow et al., 1992; Dieckmann et al., 1995; Dieckmann and Law, 1996; Geritz et al., 1997, 1998; Vincent and Brown, 2005; Brown et al., 2007).

From the point of view of the evolution of dispersal, it is possible for several rates of dispersal to coexist. In a population with polymorphic dispersal rates, the mean value, and thus the relative proportions of each dispersal type, may vary over time. And so, dispersal and dynamics are intrinsically entwined (Doebeli, 1995).

Holt and McPeek (1996) studied the evolution of dispersal in a two-patch, single-species environment where the underlying single-patch dynamics were chaotic. They showed not only that
dispersal will evolve, but also that the rate of dispersal will evolve to an evolutionary saddle at which point there will be selection for both higher and lower values of the trait. The final evolutionary endpoint is dynamic with the proportion of the high dispersal trait varying over time (figure 1, Holt and McPeek, 1996), our figure 4.1. In this case, dispersal evolves due to the fitness differences between patches precipitated by the underlying chaotic population dynamics.

Our goal here is to explore how the ecological dynamics of species-species interactions and the evolutionary dynamics of dispersal affect one another. Johst et al. (1999) studied the evolution of dynamic complexity and dispersal on a lattice and found that there was selection for greater complexity (phenotypes that drove the system to chaos were favored) and there evolved a similar dispersal polymorphism as that described in Holt and McPeek (1996). Taken together, these studies suggest that the evolution of dispersal in single-species systems with complex dynamics will favor a polymorphic population of very low and very high dispersers.

But, how does the presence of a predator affect the evolution of prey dispersal? The only multi-species studies of the evolution of dispersal of which I am aware are van Baalen and Sabelis (1993) and Křivan (1997). van Baalen and Sabelis (1993) studied the Nicholson-Bailey model (Nicholson, 1933; Nicholson and Bailey, 1935) to discern whether the conditions for ecological stability could be met if the predator and prey species were allowed to coevolve. They found that stability required either low prey fecundity or many patches of low quality for the prey. Křivan (1997) used a Lotka-Volterra two-patch model to show that adaptive dispersal (of both prey and predator) leads to more stable dynamics. Both of these studies examined the effects of predator-only dispersal, but neither examined prey-only dispersal. Nor did either of these studies look beyond stable or periodic dynamics or examine movement rates per se. I intend to extend models such as (4.1) and (4.2) to find out how the presence of a predator affects the evolution of prey dispersal when the prey-only patch dynamics are chaotic. Going forward, I will explore the evolutionary stability of different information-use strategies in these complex dynamical regimes and measure the eco-evolutionary dynamics of optimal habitat choice.
4.2 A study of several dynamical models

4.2.1 The model of Holt and McPeek (1996)

As a starting point for these investigations, consider the set of difference equations (4.3) used by Holt and McPeek (1996) in their analysis of the evolution of dispersal in a single-species two-patch system. We will refer to Holt and McPeek (1996) as HM for the remainder of this chapter.

\[
N'_1 = (1 - e_N) \cdot W(N_{T1}) \cdot N_1 + m_N \cdot e_N \cdot W(N_{T2}) \cdot N_2
\]  

(4.3a)

\[
N'_2 = (1 - e_N) \cdot W(N_{T2}) \cdot N_2 + m_N \cdot e_N \cdot W(N_{T1}) \cdot N_1
\]  

(4.3b)

\[
M'_1 = (1 - e_M) \cdot W(N_{T1}) \cdot M_1 + m_M \cdot e_M \cdot W(N_{T2}) \cdot M_2
\]  

(4.3c)

\[
M'_2 = (1 - e_M) \cdot W(N_{T2}) \cdot M_2 + m_M \cdot e_M \cdot W(N_{T1}) \cdot M_1
\]  

(4.3d)

where \( N_i \) is the abundance of species \( N \) in patch \( i \), and the prime ('') represents abundance at the next time step. \( M_i \) is a second species identical to the first except perhaps for its dispersal rate. Then, \( N_{Ti} \) represents the total abundance of species in patch \( i \), i.e., \( N_{Ti} = N_i + M_i \). \( e_N \) (\( e_M \)) represents the unconditional dispersal rate (i.e., discrete diffusion) and \( m_N \) (\( m_M \)) is the probability...
of survival for traveling between patches for species \( N(M) \). \( W \) is the per capita growth rate (i.e., instantaneous fitness) given by

\[
W(N_{Ti}) = \exp(r(1 - \frac{N_{Ti}}{K_i}))
\]  \hspace{1cm} (4.4)

where \( r \) is the intrinsic growth rate of the consumer and \( K_i \) is the carrying capacity of patch \( i \) (i.e., the Ricker model, Ricker (1954)). One could interpret these equations as describing either two competitors or one species and a variant of that species competing in a two-patch environment for a common resource (Holt and McPeek, 1996). Note that this model can be easily extended to describe the interactions of an arbitrary number of variants. In describing discrete growth, \( x' = f(x) \), we adopt the standard biological notation for instantaneous growth rate, \( W \), instead of the more common mathematical notation, \( f \), for the rest of this chapter.

Simulations of (4.3) demonstrate that the value of \( r \), and thereby the complexity of the single-patch population dynamics, plays a role in whether dispersal evolves or not (Holt and McPeek, 1996). That is, chaotic population dynamics create sufficient fitness variations between patches so that a mutant with a positive dispersal rate can cause the extinction of a sessile resident. It is well-known that the dynamic complexity of the difference equation \( N' = N \cdot W(N) \), where \( W(N) \) is the per capita growth function (4.4), depends on the value of the intrinsic growth rate \( r \) (May, 1976). For \( r < 2 \), there exists a single asymptotically stable equilibrium. For \( r \geq 2 \), the equilibrium undergoes a series of period-doubling bifurcations that causes the population dynamics to become increasingly oscillatory with ever-greater periods as \( r \) is increased, finally leading to chaotic dynamics for \( r > 2.69 \) (Oster and Guckenheimer, 1975; Oster et al., 1976). We show in figure 4.2 how the population dynamics of the two-patch system evolve as the intrinsic growth rate \( r \) is changed. Note that the threshold for chaos occurs at a higher value of \( r \) in the two-patch system with unconditional movement than in the traditional single-patch model, thereby indicating that the effective birth rate for a species moving unconditionally is lower than for a species that does not move. That is, dispersal lowers the overall growth rate of the system (Ruxton, 1993; Doebeli, 1995). Although any value of \( r \in [2.69, 2.72] \) yields chaotic dynamics in the system without dispersal, we
see from figure 4.2 that values of $r$ in this range lead to periodic behavior in the system with dispersal. Incidentally, Oster et al. (1976) note that assortative mating (in a single patch) has a similar effect on lowering the effective birth rate and thus raising the value of $r$ for which the population experiences chaotic dynamics. In that model, the reproductive rate for parents with quantitative traits $x_1$ and $x_2$ is a decreasing function of $|x_1 - x_2|$. Thus, although parents with more similar traits will have a growth rate close to $r$, the presence of genetic variance leads directly to a lower overall effective birth rate (Oster et al., 1976, pp. 369-70).

It is well-known for equilibrium systems that the single-species growth rate is maximized when dispersal is balanced (McPeek and Holt, 1992), but it is still unclear mathematically why dispersal is favored when population dynamics are chaotic. This is likely an effect of how average fitnesses are calculated over time and space (Holt and McPeek, 1996).

Certainly, it is instructive from a “first principles” point of view to understand single-species dispersal. But, quite often individuals do not exist in isolation. They compete for resources, prey upon others, and cooperate with others. These ecological interactions affect the relative reproductive success of organisms in arguably a more important way than does dispersal, however dispersal obviously affects the location and participants involved in any ecological interaction. Therefore, these ecological processes ought to be studied in tandem with dispersal. As we have seen here and in chapters 2 and 3, dispersal can play an important role in determining “who wins.” The results of HM on the evolution of dispersal motivate us to study how the presence of predators might affect the evolution of prey dispersal.

4.2.2 Analysis of a single-patch predator-prey map

To gain some intuition on the types of behavior we might expect from the addition of a predator to (4.3), we briefly analyze the single-patch equations

$$N' = \exp(r(1 - \frac{N}{K}) - bP)N \quad (4.5a)$$

$$P' = \max(0, 1 + bcN - d)P \quad (4.5b)$$
Figure 4.2: (A) Bifurcation plot of prey abundance summed across two patches for equation (4.3). $r$ varies from 1.95 to 3. (B) Maximum Lyapunov exponent for equation (4.3) as a function of $r$. Values greater than zero indicate chaos. Parameters: $r = 3$, $K_1 = 100$, $K_2 = 50$, $e_N = e_M = 0.15$, $m = 1$, initial conditions are $(9.5, 9.5, 0, 0)$.

where $N$ is the abundance of prey, $P$ is the abundance of predators, and the prime (') represents abundance at the next time step. $r$ is the intrinsic growth rate of the prey, $K$ is the carrying capacity, $b$ is the death rate of the prey due to predation, $c$ is the conversion efficiency of the predator, and $d$ is the natural death rate of the predator. Equation (4.5a) can be expressed as $N' = b(N)s(P)$ where $b(N)$ is the per capita birth rate each generation and $s(P)$ is the survival rate (by escaping predation) (see equation (2), Getz, 1996). This equation is reminiscent of the rate of a host escaping parasitism in the Nicholson-Bailey model (Nicholson and Bailey, 1935). Equations similar to (4.5b) (e.g., $N_{t+1} = N_t(1 + r[1 - \frac{N_t}{K}])$) have been considered in May (1974). Preliminary observations using a similar form of (4.5b) (namely, $P' = P \exp(bcN - d)$) are yielding qualitatively similar results.

There are two or three relevant equilibria depending on the sign of $(1 - \frac{d}{bcK})$. If this is positive, then there are three equilibria given by

$$E_0 = (0, 0),$$
$$E_1 = (K, 0),$$
$$E_2 = \left(\frac{d}{bc}, \frac{r}{b}(1 - \frac{d}{bcK})\right).$$

$E_0$ is unstable for all positive $r$. $E_1$ is asymptotically stable when both $r < 2$ and $1 - \frac{d}{bcK} < 0$. It is
unstable otherwise. \( E_2 \) exists in the positive quadrant only when \((1 - \frac{d}{bcK}) > 0\). This equilibrium is asymptotically stable when

\[
d < \frac{1}{2} \left[ bcK - 2 + \sqrt{4 - 4bcK + (bcK)^2 + \frac{16bcK}{r}} \right]
\]

(4.9)

From (4.9), we see that the interior equilibrium, \( E_2 \), will be asymptotically stable for small values of \( d \). Choosing the parameter values \( b = 0.1, c = 0.03, K = 100, r = 3 \), we see that \( d \) must satisfy \( d < 0.209481 \) for (4.9) to hold (compare with figure 4.3). As \( d \) increases from small values, the dynamics become more complex as in the single-species case. The increase in the predator’s death rate serves to effectively increase the growth rate of the prey (by reducing the effect of predation) leading to potentially unstable oscillations. A bifurcation diagram for \( d \), the predator death rate, for (4.5) demonstrates that there is a period-doubling route to chaos (figure 4.3, panel A). We also

include in figure 4.3, panel B, the bifurcation diagram for \( r \) for the same equation (4.5) where we see that chaos does not occur when the predator’s death rate is large, \( d = 0.25 \), until approximately \( r > 3.01 \).

When the prey and predator are at the \( E_2 \) equilibrium, increasing \( r \) will destabilize the prey equilibrium. In turn, this will cause the predator equilibrium to be unstable; we could calculate

![Figure 4.3: Prey abundance in the single-patch predator-prey system given by (4.5). Parameter values: \( K = 100, b = 0.1, c = 0.03 \). (A) Bifurcation plot for equation (4.5), \( t = 100000 \). \( d \) varies from 0.20 to 0.26, \( r = 3 \). (B) Bifurcation plot for equation (4.5), \( t = 100000 \). \( r \) varies from 2.8 to 3.1, \( d = 0.25 \). The presence of the predator lowers the effective birth rate of the prey which causes bifurcations to occur at higher values of \( r \) than in the absence of the predator. Compare with figure 4.2.](image)
this value of \( r \) from (4.9). However, to gain some understanding of how this model differs from (4.2), we analyze the stability of \( E_2 \) and remark upon an essential difference.

Consider the prey-only equation given by \( N' = G(N) = N \exp(r(1 - \frac{N}{K})) \). The equilibrium \( N^* \) will be asymptotically stable if \(|G'(N^*)| < 1\) (for functions \( F \) and \( G \), the \( ' \) denotes \( \frac{d}{dN} \)). We can rewrite (4.5a) as \( N' = F(N, P^*) = e^{-bP^*}G(N) \). \( E_2 \) loses stability when \( |F'(N^*, P^*)| = 1 \), and

\[
F'(N^*, P^*) = \exp(r(1 - \frac{N^*}{K}) - bP^*)(1 - \frac{r}{K}N^*) \\
= \exp(-bP^*)\exp(r(1 - \frac{N^*}{K}))(1 - \frac{r}{K}N^*) \\
= \exp(-bP^*)G'(N^*) \tag{4.10}
\]

from which we see that since \( \exp(-bP^*) \leq 1 \), the effect of the predator is to increase the value of \( r \) at which \( E_2 \) becomes unstable.

How does this differ from the complexity-reducing behavior of (4.2)? As remarked in Stone and Hart (1999, pg. 229), the addition of \( c \) in that model shifts the return map \( (F) \) plotted on the \( x' - x \) axes up \( "c" \). Since this map is typically concave up for large \( x \), the slope of the map where it intersects \( x' = x \) is much flatter than in the absence of immigration (Stone and Hart, 1999, their figure 2). The presence of immigration increases the limiting behavior of density-dependent growth of the prey, thereby lowering its effective growth rate. By contrast, in (4.5), we see from (4.10) that introducing the predator multiplies the return map, which contracts \( F \). If \( F \) is concave down where the map intersects the 45°-line (i.e., where \( N' = N \)), then the slope of \( F \) at the point of intersection will be reduced due to the presence of the predator. In short, the presence of the predator reduces the prey’s effective growth rate thus avoiding the paradox of enrichment (Rosenzweig, 1971). Although the dynamical effects of these “chaos control” mechanisms are similar (also see Doebeli (1995)), the biological and mathematical reasons for them are significantly different.
Now we are prepared to modify the original system of HM, equations (4.3), to include a predator with a linear functional response. The difference equation model is

\[ N'_1 = (1 - e_N) \cdot W(N_{T1}, P_1) \cdot N_1 + m_N \cdot e_N \cdot W(N_{T2}, P_2) \cdot N_2 \quad (4.11a) \]

\[ N'_2 = (1 - e_N) \cdot W(N_{T2}, P_2) \cdot N_2 + m_N \cdot e_N \cdot W(N_{T1}, P_1) \cdot N_1 \quad (4.11b) \]

\[ M'_1 = (1 - e_M) \cdot W(N_{T1}, P_1) \cdot M_1 + m_M \cdot e_M \cdot W(N_{T2}, P_2) \cdot M_2 \quad (4.11c) \]

\[ M'_2 = (1 - e_M) \cdot W(N_{T2}, P_2) \cdot M_2 + m_M \cdot e_M \cdot W(N_{T1}, P_1) \cdot M_1 \quad (4.11d) \]

\[ P'_i = \max(0, [1 + N_{T_i} \cdot b_i \cdot c - d])P_i \quad (i = 1, 2) \quad (4.11e) \]

where \( N_i \) \((M_i)\) is the abundance of prey species \( N \) \((M)\) in patch \( i \), \( P_i \) is the abundance of predators in patch \( i \), and the prime ('') represents abundance at the next time step. As before, \( N_{T_i} = N_i + M_i \).

\( r \) is the intrinsic growth rate of the prey, \( K_i \) is the carrying capacity of patch \( i \), \( m_N(m_M) \) is the survival rate of prey species \( N \) (prey species \( M \)) traveling between patches, \( b_i \) is the death rate of the prey due to predation, \( d \) is the natural death rate of the predator, \( c \) is the conversion efficiency of the predator, and

\[ W_i := W(N_{T_i}, P_i) = \exp(r(1 - N_{T_i} / K_i) - b_i \cdot P_i) \quad (4.12) \]

is the per capita fitness of prey in patch \( i \). We will take \( m_N = m_M = 1 \) in all of our analysis. Note that the predator does not move, so it can go extinct in one or both patches.

We can solve for the nontrivial equilibrium of (4.11) when \( m = 1 \). At an equilibrium, (4.11e) yields \( N_i^* + M_i^* = \frac{d}{\partial b_i} \). When \( e_N = \frac{1}{2} \), we can easily solve equations (4.11a) and (4.11b) to discover that \( N_1^* = N_2^* \). Then, combining these facts, we find that

\[ \frac{d}{\partial b_i} = N_2^* + M_2^* \]

\[ = N_1^* + M_2^* \]

but \( \frac{d}{\partial b_i} = N_1^* + M_1^* \), from which it follows necessarily that \( M_1^* = M_2^* \). By adding and subtracting
equations (4.11a) and (4.11b) in turn, we find that \( W_1 + W_2 = 2 \) and \( W_1 - W_2 = 0 \). Thus, we can conclude that \( P_i^* = r(1 - \frac{d}{e_i K_i})/b_i \).

When \( e_i \neq \frac{1}{2} \), we can also show that \( N_1^* = N_2^* \) and \( M_1^* = M_2^* \), but it is slightly more involved, as we see below. Dividing equations (4.11a)-(4.11d) at equilibrium by the respective dynamic variables and simplifying leads to

\[
\begin{align*}
\frac{N_2^*}{N_1^*} &= \frac{1 - (1 - e_N)W_1}{e_N W_2} \\
\frac{N_1^*}{N_2^*} &= \frac{1 - (1 - e_N)W_2}{e_N W_1} \\
\frac{M_2^*}{M_1^*} &= \frac{1 - (1 - e_M)W_1}{e_M W_2} \\
\frac{M_1^*}{M_2^*} &= \frac{1 - (1 - e_M)W_2}{e_M W_1}
\end{align*}
\] (4.13a-d)

Equating (4.13a) with the reciprocal of (4.13b) and also (4.13c) with the reciprocal of (4.13d) and simplifying, we have

\[
(1 - e_N)(W_1 + W_2) - (1 - 2e_N)W_1 W_2 = 1 \quad (4.14a)
\]
\[
(1 - e_M)(W_1 + W_2) - (1 - 2e_M)W_1 W_2 = 1 \quad (4.14b)
\]

where not necessarily \( e_N = e_M \). Thus, subtracting these two equations and simplifying gives

\[
W_1 + W_2 = 2W_1 W_2 \quad (4.15)
\]

Using (4.15) to substitute for \( W_1 + W_2 \) in one of equations (4.14) yields \( W_1 W_2 = 1 \). Now, \( W_i \) is an exponential function of the form \( e^{A_i} \). Thus, \( A_1 + A_2 = 0 \). Then, either by geometric or algebraic arguments, the statement \( e^{A_1} + e^{A_2} = 2 \) necessarily implies that \( A_i = 0 \). Therefore, \( W_i = 1 \), \( N_i^* + M_i^* = \frac{d}{\delta_i} \) and, incidentally, we recover the previous expression for \( P_i^* = \frac{r}{b_i}(1 - \frac{d}{e_i K_i}) \).

Since \( W_i = 1 \), we see from equations (4.11) that \( N_1^* = N_2^* \) and \( M_1^* = M_2^* \). This implies also, by subtracting \( N_2^* + M_2^* = \frac{d}{\delta_2} \) from \( N_1^* + M_1^* = \frac{d}{\delta_1} \) that \( \frac{d}{\delta_1} = \frac{d}{\delta_2} \), so \( b_1 = b_2 \). Thus, no interior equilibrium exists unless \( b_1 = b_2 \) which, by virtue of \( N \) and \( M \) differing only in \( e_i \), holds for our study. The exact values of \( N_i^* \) and \( M_i^* \) depend on the initial conditions.
4.2.3.1 Both prey disperse at the same rate: $e_N = e_M$

Our numerical results indicate that unconditional dispersal has a large effect on the persistence of the two-patch predator-prey system. At low dispersal values, $e_i \approx 0.05$, the predator population in the second patch goes extinct, presumably because there are not enough prey in the second patch to support a predator population in this patch (recall that the predators are sessile). This view is supported by the phase portraits of the predator and prey in the first patch (figure 4.4). As $e_i$ is increased, the dynamics become more organized. Greater mixing of prey between patches increases their numbers in the second patch. This helps support a predator population there which reduces the prey’s overall growth rate leading to less complex dynamics.

When $e_i = 0.06$, one can clearly see the stabilizing effect that the predator in the second patch has on the prey in that patch. As $e_i$ is reduced to below $e_i = 0.06$, the predator in the second patch goes extinct (figure 4.5) and the prey abundances again become chaotic. Just prior to this extinction however, there is a noticeable change in the quality of the phase portraits between $e_i = 0.07$ and $e_i = 0.08$ and again between $e_i = 0.08$ and $e_i = 0.10$ (figures 4.4 and 4.6).

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure4_4.png}
\caption{Predator abundance in patch 1. $e_N = e_M = e$. (A) $e = 0.15$, (B) $e = 0.2$, (C) $e = 0.25$, (D) $e = 0.35$. Parameter values: $r = 2.8$, $K_1 = 1000$, $K_2 = 500$, $m = 1$, $b = 0.1$, $c = 0.03$, $d = 1$.}
\end{figure}
4.2.3.2 Prey disperse at different rates: $e_N \neq e_M$

We explored numerically what occurs when the prey are identical except for their random movement rate. We fixed $b_i = 0.1, c = 0.03, K_1 = 1000, K_2 = 500$. Systematically, we varied $r, e_N, e_M, d$, and the initial conditions. We used a set of ten different initial conditions (some were symmetric, some were anti-symmetric or random). Parameter values that we explored factorially are

- $r = 1, 2, 3, 4$
- $d = 0.80, 0.90, 1.00, 1.10$
- $e_i = 0.01, 0.10, 0.25, 0.50$

In general, we discovered that the predator persists for almost the same sets of parameters regardless of initial conditions. The one exception to this was that the predator in the second patch always went extinct when initial abundances of prey in the second patch were low and $d = 1.10$. When
Figure 4.6: Predator abundance in patch 1. $e_N = e_M = e$. $e$ increases from 0.07 to 0.08. Parameter values: $r = 3$, $K_1 = 1000$, $K_2 = 500$, $m = 1$, $b = 0.1$, $c = 0.03$, $d = 1$.

$r = 4$, the predator goes extinct when $d \geq 0.9$ except when $e_N = e_M = 0.01$. Thus, at higher complexity, a greater mortality rate as well as some degree of random prey movement combine to cause extinction of the predator.

We see qualitatively different results regarding the evolution of dispersal when the diffusion rates of the two prey are unequal. That is, the presence of the predator fundamentally changes the results of HM. Recall from section 4.1 that we described the presence of an evolutionary saddle in the original model of HM. In that model, whenever $e_N > 0.125$, there was selection for lower levels of dispersal. And, as long as one species was present with $e_N > 0.125$, a second species with $e_M < 0.125$ could increase, forming a coalition that would evolve to $e_N = 0.50$ and $e_M = 0.01$. The striking result here is that when $r = 3$, $e_N > e_M$, and $d < 1.0$, the mutant (playing $e_M$) cannot invade (figure 4.7). Apparently, the higher value of $e_N$ promotes the presence of the predator in both patches thereby making it impossible for a mutant with a lower value of $e_M$ to increase when rare.

The presence of the predator can also change the dynamics and positively affect the presence of both variants of prey. In the original model of HM, two variants with $e_N = 0.25$ and $e_M = 0.50$ could not coexist. The variant with the smaller dispersal rate could exclude the faster disperser. Note that they used carrying capacities ten times smaller than ours, but their prey-only results still hold here. When we introduce a predator into both patches, both prey variants can coexist.
Figure 4.7: Presence of the mutant after 20000 times steps (black represents absence). Parameter values: $K_1 = 1000$, $K_2 = 500$, $m = 1$, $b = 0.1$, $c = 0.03$, $r$ varies, $d$ varies, $e_i$ varies. The $12 \times 12$ image contains $9 \times 4 \times 4$ subimages. In each subimage, the value of $e_N$ changes in each row and the value of $e_M$ changes in each column. Each $e$ takes on the values 0, 0.10, 0.25, 0.50 increasing with increasing row or column number within each subimage.

(figure 4.8; $r = 3$, $d = 1.0$). The presence of the predator facilitates this coexistence. Interestingly, the predator’s death rate affects the dynamical complexity of this system. When the predator death rate is high enough (it works for $d = 1.05$), the dynamics go to an equilibrium. This is most likely due to the multiplicative effect of $\exp(-bP)$ as described in our analysis of the single-patch predator-prey map (4.5). We show in figure 4.9 the effect that increasing $d$ has on species abundances.

4.3 Discussion

We see that the presence of a predator impacts the evolution of prey dispersal by (1) causing prey extinctions where in the absence of the predator, prey coexistence is expected, and (2) facilitating coexistence of prey with different dispersal strategies when coexistence was not possible without the predator. Although in one case, the predator is a keystone predator (Amarasekare, 2010) that allows the coexistence of the competing prey species, we see that predator presence does not a priori facilitate or prevent coexistence.

The presence of a predator can also affect the dynamics of this system. This depends on the predator’s death rate. As the predator’s death rate enters a critical region in parameter space,
Figure 4.8: Presence of both the resident and the invader after 20000 times steps (black represents coexistence).

Parameter values: $K_1 = 1000$, $K_2 = 500$, $m = 1$, $b = 0.1$, $c = 0.03$, $r$ varies, $d$ varies, $e_i$ varies. The $12 \times 12$ image contains $9 \cdot 4 \times 4$ subimages. In each subimage, the value of $e_N$ changes in each row and the value of $e_M$ changes in each column. Each $e$ takes on the values 0, 0.10, 0.25, 0.50 increasing with increasing row or column number within each subimage. Notice the positive effect that complexity and the predator death rate have on coexistence.

The equilibrium becomes stable. On one side of this critical region, the predator exists with the prey species that is the faster disperser, and on the other side of this region, the prey species that is the slower disperser survives alone. This last result echoes the well-known single-species result that in the absence of temporal heterogeneity, the slower species is more adaptive (Dockery et al., 1998). In some sense then, the predator’s death rate controls who survives and also controls the overall complexity of the population dynamics. This type of control differs from Doebeli (1995) in that chaotic dynamics are not controlled by the focal species but rather by a species from another trophic level. We found similar behavior in a continuous-time tri-trophic model studied by Hastings and Powell (1991) and Klebanoff and Hastings (1994). These results on dynamics and coexistence may have implications for the management of natural resources.

4.4 Future work

The limited, but interesting, results we have obtained so far point towards many unanswered questions. We hope to explore the following ideas in the future.

(1) We have only scratched the surface in analyzing the two-patch predator-prey map (4.11) and
the effect of the predator death rate on the dynamics of the system. Our system is effectively a set of heterogeneous diffusively-coupled chaotic oscillators with time-varying coupling strengths. There is some theory pertaining to using diffusive oscillators to control chaos (mentioned in Pecora et al., 1997), but to our knowledge this has not been studied previously from a biological viewpoint. Going forward, we would like to explore the mathematical generality of the results from this chapter.

(2) We have begun exploring how different information-use strategies might affect the composition of the two-patch predator-prey map (4.11). It may be interesting to explore: if there is a cost to acquiring information from the other patch, then fitness-based movement would pay a cost that habitat-based movers or unconditional dispersers do not. Then, how does the underlying ecological dynamics affect the optimality of information use? How do our conclusions change with predator movement?

(3) What can be said about the bifurcation structure of this model? Specifically, what is occurring throughout the critical region in the $d$ parameter space? Also, what is the bifurcation structure of the apparent break-up of the prey-predator attractor as $e$ changes from $e = 0.07$ to $e = 0.08$ and the subsequent re-establishment when $e = 0.15$?

The answers to these questions will add to our understanding of the evolution of habitat-selection strategies and the dynamical interplay between ecology and evolution.
Figure 4.9: (A) Predator abundance in patch 2. The predator goes extinct in both patches at about $d = 1.23$. (B) Prey with the lower movement rate is extinct for $d < 1$. The presence of the second prey stabilizes the chaotic dynamics. (C) and (D): Prey with the greater movement rate goes extinct near $d = 1.23$. The slower prey is the only species that survives when $d > 1.23$. Parameter values: $r = 3$, $K_1 = 1000$, $K_2 = 500$, $m = 1$, $b = 0.1$, $c = 0.03$, $e_1 = 0.5$, $e_2 = 0.25$. 
Chapter 5

Conclusion

Analyzing spatial ecological models is difficult. So why add evolution? Early mathematical models of ecological processes had fixed parameters that did not vary in time or space (e.g., Nicholson, 1933). Experiments were conducted, parameters were estimated, and the quality of the model was judged by how well it fit the data. Spatial ecological modeling arrived in the 1950's when Skel-lam (1951) studied the speed of species invasions. By the 1970’s, three separate events important to modern ecological modeling were occurring. First, the study of spatial models was becoming more commonplace (Levin, 1976). Second, Robert May and others began to study simple ecological models with complex dynamics (May, 1972b,a, 1973; Rocklin and Oster, 1976; May, 1976; Oster et al., 1976; Guckenheimer et al., 1977; May, 1977; Asmussen, 1979). Third, Maynard Smith and Price (1973) introduced and extended the concepts of Nash equilibria to biology. This last event spurred the integration of the evolution of dispersal into ecological models (e.g., Hamilton and May, 1977; Comins et al., 1980). In the late 1980’s and mid-1990’s, evolutionary game theory was in full swing (Dieckmann et al., 1995; Vincent and Brown, 2005), and two different camps, one primarily in Europe, and the other in the U. S., began studying in earnest the relationship between ecology and evolution.

We are excited to be a very small part of this revolution in evolution. Our work has shown that ignoring fitness, in some cases, may be the habitat-selection strategy that maximizes fitness. We have shown that costs will cause the distribution resulting from the single-species dispersal ESS to be other than the ideal free distribution. Lastly, we have shown that information-use strategies
in predator-prey systems may be extremely sensitive to parameter values, and observed that there exists mathematically interesting feedback between the underlying ecological dynamics and the evolution of optimal habitat selection. Future challenges include qualifying how resource dynamics affect our conclusions about the non-adaptiveness of fitness-based movement, studying how the evolution of animal behavior affects species interactions across space, and discovering otherwise how these results fit into community ecology.

In answer to the question posed at the beginning of this chapter, we add evolution to our models because doing so allows us to ask questions like: Why does dispersal evolve? How do predator and prey coevolve? What kinds of information do organisms use to guide movement? Integrating evolution into models of ecology empowers us to answer long-standing questions in competitive interactions (Rael et al., 2010) and reveal interesting, novel dynamics in predator-prey interactions (Yoshida et al., 2009). As technologies and eco-evolutionary theory improve, experimentalists will be able to test hypotheses generated by theory, and their results will feed back to the development of new theory. Given the current level of interest in eco-evolutionary theory, we anticipate that mathematics will continue to play a fundamental role in future modeling advances in ecology and evolution.
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Appendix A

Convergence stability derivation

The sufficient condition for convergence stability (1.5) given in chapter 1 is applicable to one-dimensional traits. Abrams et al. (1993) give convergence stability conditions for two-dimensional traits, which we rederive here. More generally, convergence stability conditions for strategies of arbitrary dimensions can be found in these sources: Leimar (2005, 2009); Apaloo and Butler (2009).

This derivation is nothing more than a Taylor expansion about an evolutionarily singular strategy, \( \mathbf{x}^* \), when the strategy is a two-dimensional vector. Thus, if the genetic changes that affect trait \( y_i \) do not affect trait \( y_j \), we see that
\[
s_{\mathbf{x}}(\mathbf{y}) = s_{\mathbf{x}}(\mathbf{x}^*) + \begin{bmatrix} \frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial y_1} \\ \frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial y_2} \end{bmatrix}^T (\mathbf{y} - \mathbf{x}^*) + \frac{1}{2} (\mathbf{y} - \mathbf{x}^*)^T \mathbf{J}(\mathbf{y} - \mathbf{x}^*) + \text{H. O. T.} \quad (A.1)
\]

where \( \mathbf{y} - \mathbf{x}^* = \begin{bmatrix} y_1 - x_1^* \\ y_2 - x_2^* \end{bmatrix} \), H. O. T. represents the neglected higher-order terms, and the matrix \( \mathbf{J} \) is the Jacobian matrix of the selection gradient (Leimar, 2005)
\[
\mathbf{J} = \begin{bmatrix} \frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_1^2} + \frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_1 \partial x_1} & \frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_1 \partial y_2} + \frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_1 \partial x_2} \\ \frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_2 \partial y_1} + \frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_2 \partial x_1} & \frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_2^2} + \frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_2 \partial x_2} \end{bmatrix}.
\]

All derivatives are evaluated at the singular strategy, i.e., \( \mathbf{y} = \mathbf{x} = \mathbf{x}^* \). By definition, \( s_{\mathbf{x}}(\mathbf{x}) = 0 \) since this represents the growth rate of a resident on its ecological attractor. Given an evolutionarily singular strategy \( \mathbf{x}^* \), where \( \mathbf{x}^* = [x_1^*, x_2^*]^T \), the selection gradient must be zero, i.e., \( \frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial y_1} |_{y_1 = x_1^*} = \frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial y_2} |_{y_2 = x_2^*} = 0 \). The ability of a mutant to invade when rare then depends on the maximum eigenvalue of \( \mathbf{J} \).
If traits $y_1$ and $y_2$ are genetically linked, then the selection gradient of $y_2$ will affect the direction of the evolution of trait $y_1$. Thus, the second term in (A.1) becomes

$$
\begin{bmatrix}
g_{11} \frac{\partial s_x(y)}{\partial y_1} + g_{12} \frac{\partial s_x(y)}{\partial y_2} \\
g_{21} \frac{\partial s_x(y)}{\partial y_1} + g_{22} \frac{\partial s_x(y)}{\partial y_2}
\end{bmatrix}
\cdot (y - x^*)
$$

where $g_{ij}$ represents the effect that a change in trait $j$ has on trait $i$ (i.e., the additive genetic variances and covariances) (Abrams et al., 1993). The matrix $J$ becomes

$$
J = \begin{bmatrix}
g_{11} \left( \frac{\partial^2 s_x(y)}{\partial y_1^2} + \frac{\partial^2 s_x(y)}{\partial y_1 \partial x_1} \right) + g_{12} \left( \frac{\partial^2 s_x(y)}{\partial y_2 \partial y_1} + \frac{\partial^2 s_x(y)}{\partial y_2 \partial x_1} \right) & g_{11} \left( \frac{\partial^2 s_x(y)}{\partial y_1 \partial y_2} + \frac{\partial^2 s_x(y)}{\partial y_1 \partial x_2} \right) + g_{12} \left( \frac{\partial^2 s_x(y)}{\partial y_2^2} + \frac{\partial^2 s_x(y)}{\partial y_2 \partial x_2} \right) \\
g_{21} \left( \frac{\partial^2 s_x(y)}{\partial y_1^2} + \frac{\partial^2 s_x(y)}{\partial y_1 \partial x_1} \right) + g_{22} \left( \frac{\partial^2 s_x(y)}{\partial y_2 \partial y_1} + \frac{\partial^2 s_x(y)}{\partial y_2 \partial x_1} \right) & g_{21} \left( \frac{\partial^2 s_x(y)}{\partial y_1 \partial y_2} + \frac{\partial^2 s_x(y)}{\partial y_1 \partial x_2} \right) + g_{22} \left( \frac{\partial^2 s_x(y)}{\partial y_2^2} + \frac{\partial^2 s_x(y)}{\partial y_2 \partial x_2} \right)
\end{bmatrix}
$$

This can be written more compactly (where we make the assumption that $g_{12} = g_{21}$) as

$$
J = \begin{bmatrix}
g_{11} F_{11} + g_{12} F_{21} & g_{11} F_{12} + g_{12} F_{22} \\
g_{12} F_{11} + g_{22} F_{21} & g_{12} F_{12} + g_{22} F_{22}
\end{bmatrix}
$$

where $F_{12} := \frac{\partial^2 s_x(y)}{\partial y_1 \partial y_2} + \frac{\partial^2 s_x(y)}{\partial y_1 \partial x_2}$. The necessary conditions for stability of a resident-only system then depends on the eigenvalues of $J$. To apply this to our model (2.2), we can make the notational substitutions where, in short, $x$ and $y$ correspond to resident and mutant traits, and 1 and 2 correspond to $m$ and $\tau$. Then,

$$
m_R := x_1
$$

$$
\tau_R := x_2
$$

$$
m_M := y_1
$$

$$
\tau_M := y_2
$$

$$
g_{m, m} := g_{11}
$$

$$
g_{m, \tau} := g_{12}
$$

$$
g_{\tau, m} := g_{21}
$$

$$
g_{\tau, \tau} := g_{22}
$$
With these substitutions, the necessary conditions for stability become

\[ F_{mm}g_{m,m} + (F_{\tau m} + F_{m\tau})g_{m,\tau} + F_{\tau\tau}g_{\tau,\tau} < 0 \]
\[ (g_{m,m}g_{\tau,\tau} - (g_{m,\tau})^2)(F_{mm}F_{\tau\tau} - F_{m\tau}F_{\tau m}) > 0 \]

which are equations (2.4) and (2.5) in the text, chapter 2. In chapter 2, final mutant abundances are used as a proxy for mutant fitness whereas in chapter 3, section 3.6, we explain the convergence results when using the per capita growth rate of a mutant when rare.
Appendix B

Convergence results

We include here derivative estimates using a step size of $10^{-4}$ around the particular optimal strategy $(m^*, \tau^*) = (0.6, 0.5)$, other parameters as in table 2.1 in the main text. We denote the evaluation of a derivative at $(m^*, \tau^*)$ by $|\cdot|_\ast$. $F$ represents final mutant abundance.

Substituting the values from table B.01 into conditions (2.4) of the main text gives:

$$
\left[ \left( \frac{\partial^2 F}{\partial m^2_M} + \frac{\partial^2 F}{\partial m_M \partial m_R} \right) \cdot g_{m,m} + \left( 2 \cdot \frac{\partial^2 F}{\partial m_M \partial \tau_M} + \frac{\partial^2 F}{\partial m_M \partial \tau_R} \right) \cdot g_{m,\tau} + \left( \frac{\partial^2 F}{\partial \tau^2_M} + \frac{\partial^2 F}{\partial \tau_M \partial \tau_R} \right) \cdot g_{\tau,\tau} \right]_\ast
$$

$$
= (-3.323 \times 10^6) \cdot g_{m,m} + (4.046 \times 10^5) \cdot g_{m,\tau} + (-3.432 \times 10^6) \cdot g_{\tau,\tau} < 0
$$

Table B.01: Derivative values

<table>
<thead>
<tr>
<th>Derivative</th>
<th>Numerical Approximation</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\frac{\partial^2 F}{\partial m_M^2}$</td>
<td>$-2.787 \times 10^4$</td>
</tr>
<tr>
<td>$\frac{\partial^2 F}{\partial m_M \partial m_R}$</td>
<td>$-4.013 \times 10^4$</td>
</tr>
<tr>
<td>$\frac{\partial^2 F}{\partial \tau^2_M}$</td>
<td>$-3.295 \times 10^6$</td>
</tr>
<tr>
<td>$\frac{\partial^2 F}{\partial m_M \partial \tau_M}$</td>
<td>$2.980 \times 10^4$</td>
</tr>
<tr>
<td>$\frac{\partial^2 F}{\partial m_M \partial \tau_R}$</td>
<td>$1.095 \times 10^5$</td>
</tr>
<tr>
<td>$\frac{\partial^2 F}{\partial \tau_M \partial m_R}$</td>
<td>$2.355 \times 10^5$</td>
</tr>
<tr>
<td>$\frac{\partial^2 F}{\partial \tau_M \partial \tau_R}$</td>
<td>$-3.392 \times 10^6$</td>
</tr>
</tbody>
</table>
Substituting these values into conditions (2.5) gives:

\[
(g_{m,m} g_{\tau,\tau} - (g_{m,\tau})^2)((-3.323 \times 10^6)(-3.432 \times 10^6) -
(2.653 \times 10^5)(1.393 \times 10^5))

= (g_{m,m} g_{\tau,\tau} - (g_{m,\tau})^2)(1.137 \times 10^{13}) > 0
\]

(B.02) will hold evidently when \(g_{m,m} g_{\tau,\tau} > (g_{m,\tau})^2\), but it is unclear for what values of \(g_{m,m}, g_{m,\tau}, g_{\tau,\tau}\) will (B.01) hold.

We now show that \(g_{m,m} g_{\tau,\tau} > (g_{m,\tau})^2\) is sufficient for (B.01) to be satisfied. We change notation here for convenience of exposition. Let \(x = g_{m,m}, y = g_{m,\tau}, z = g_{\tau,\tau}\). Let \(a, b, c\) represent the coefficients of \(x, y, z\) respectively. We assume that \(a < 0, b > 0, c < 0\), since this was true in all of our simulations. Then, \(g_{m,m} g_{\tau,\tau} > (g_{m,\tau})^2\) implies that \(x \cdot z > y^2\). Thus, for any fixed \(x, y, z\), there exists an \(\epsilon > 0\) such that \(x \cdot z = y^2 + \epsilon\). (B.01) will hold if \(\max\{f(x, y, z)\} = \max\{ax + by + cz\} < 0\).

Using our initial assumption, we solve for \(y\) as a function of \(x\) and \(z\) yielding \(y = \pm \sqrt{xz - \epsilon}\). We plug this value of \(y\) into \(f\) which reduces our problem to a two-dimensional maximization problem. For reasons made clear below, we choose the positive root. A maximum will not exist when \(x = z = 0\) since by assumption \(x \cdot z > 0\). Also, if \(y = 0\), then any maximum there will satisfy \(\max\{ax + by + cz\} < 0\); therefore, we seek a maximum of \(f\) when \(x, z \in (0, \infty)\). Elementary calculus states that to find the maximum of \(f\), the following must be satisfied: (1) \(f_x = 0\), (2) \(f_z = 0\), (3) \(f_{xx} < 0\), (4) \(f_{xx} f_{zz} - (f_{xz})^2 > 0\), where the subscripts represent partial derivatives and all derivatives are evaluated at the maximum.
Straightforward differentiation yields:

\[ f_x = a + \frac{b}{2}z(xz - \epsilon)^{-1/2} \]  
\[ f_z = c + \frac{b}{2}x(xz - \epsilon)^{-1/2} \]  
\[ f_{xx} = -\frac{b}{4}z^2(xz - \epsilon)^{-3/2} \]  
\[ f_{xz} = \frac{b}{2}(xz - \epsilon)^{-1/2} - \frac{b}{4}xz(xz - \epsilon)^{-3/2} \]  
\[ f_{zz} = -\frac{b}{4}x^2(xz - \epsilon)^{-3/2} \]

Notice that \( f_{xx} < 0 \) only if we chose the positive root for \( y = \sqrt{xz - \epsilon} \) above. Also,

\[ f_{xx}f_{zz} - (f_{xz})^2 = \left(-\frac{b}{4}z^2(xz - \epsilon)^{-3/2}\right)
\left(-\frac{b}{4}x^2(xz - \epsilon)^{-3/2}\right)
- \left(\frac{b}{2}(xz - \epsilon)^{-1/2} - \frac{b}{4}xz(xz - \epsilon)^{-3/2}\right)^2
= \epsilon\left(\frac{b}{2(xz - \epsilon)}\right)^2 > 0 \]  

We find by setting (B.03) and (B.04) equal to zero that the maximum occurs when \( z = \frac{a}{c}x \).

Plugging this into \( f(x, y, z) \) and simplifying yields \( \max\{ax + by + cz\} = z(2c + b\sqrt{\frac{z}{a}}) \). For all of our simulations, \( (2c + b\sqrt{\frac{z}{a}}) < 0 \). Since \( z > 0 \), and \( f_{xx}, f_{zz} < 0 \) everywhere, we have that \( \max\{ax + by + cz\} < 0 \).

### B.1 Derivation of the optimal strategy with costs

We seek a relationship between \( m \) and \( \tau \) so that at the ecological equilibrium, the population will be distributed at the IFD. The following dynamical equations describe movement with travel
costs as described in the text:

\[
\dot{N}_1 = f(N_1; K_1) \cdot N_1 - d(N_1 - N_2(1 - k)) \\
\quad + (1 - k)m[\tau \cdot \max(0, \tilde{N}) + (1 - \tau) \cdot \tilde{K}]N_2 \\
\quad - m[\tau \cdot \max(0, -\tilde{N})]N_1
\] (B.11a)

\[
\dot{N}_2 = f(N_2; K_2) \cdot N_2 + d(N_1(1 - k) - N_2) \\
\quad - m[\tau \cdot \max(0, \tilde{N}) + (1 - \tau) \cdot \tilde{K}]N_2 \\
\quad + (1 - k)m[\tau \cdot \max(0, -\tilde{N})]N_1
\] (B.11b)

At the ecological equilibrium, \(\dot{N}_1 = \dot{N}_2 = 0\). Furthermore, at the IFD, \(f(N_1; K_1) = f(N_2; K_2)\) (which implies \(\tilde{N} = 0\)) so that we can let \(\gamma = \frac{N_1}{K_1} = \frac{N_2}{K_2}\) for some \(\gamma \in [0, 1]\). Now, we can solve for \(m^*\) and \(\gamma_s\) by straightforward algebra, yielding:

\[
m^* = \frac{d}{1 - \tau} \left(1 + \frac{K_1}{K_2}\right) \left[\frac{(K_1 + K_2)(1 - k)}{(K_1 + K_2) - kK_2}\right]
\] (B.12a)

\[
\gamma_s = 1 - k \frac{d}{r} \frac{K_1(2 - k)}{K_1 + K_2 - kK_2}
\] (B.12b)

The following dynamical equations describe movement with sensory machinery costs as described in the text:

\[
\dot{N}_1 = f(N_1; K_1) \cdot N_1 - d(N_1 - N_2) \\
\quad + m[\tau \cdot \max(0, \tilde{N}) + (1 - \tau) \cdot \tilde{K}]N_2 \\
\quad - m[\tau \cdot \max(0, -\tilde{N})]N_1 - mkN_1
\] (B.13a)

\[
\dot{N}_2 = f(N_2; K_2) \cdot N_2 + d(N_1 - N_2) \\
\quad - m[\tau \cdot \max(0, \tilde{N}) + (1 - \tau) \cdot \tilde{K}]N_2 \\
\quad + m[\tau \cdot \max(0, -\tilde{N})]N_1 - mkN_2
\] (B.13b)

Again, we let \(\gamma = \frac{N_1}{K_1} = \frac{N_2}{K_2}\) for some \(\gamma \in [0, 1]\). Now, we can solve for \(m^*\) and \(\gamma_s\) to yield:

\[
m^* = \frac{d}{1 - \tau} \left(1 + \frac{K_1}{K_2}\right)
\] (B.14a)

\[
\gamma_s = 1 - k \frac{d}{r} \cdot m^*
\] (B.14b)
provided $K_1 \neq K_2$. Notice that equation (B.14a) is the same as equation (2.3a). Notice also that in the absence of any costs, $\gamma = 1$, $N_1 = K_1$, and $N_2 = K_2$, recovering the optimal strategy (2.3a) from the main text. Since $\gamma \geq 0$, we see by equation (B.14b) that $m^* \leq \frac{r}{\xi}$, indirectly putting an upper bound on $\tau^*$. 
Appendix  C

Center manifold reduction

We begin with equations (3.6) from the text. Set $k = 0$ and $\tau_R = \tau_M = 0$. Then, this system of equations is

\[
\begin{align*}
\dot{N}_1 &= r(1 - \frac{N_1 + M_1}{K_1}) N_1 - dN_1 + (d + m_R \tilde{K}) N_2 \\
\dot{N}_2 &= r(1 - \frac{N_2 + M_2}{K_2}) N_2 + dN_1 - (d + m_R \tilde{K}) N_2 \\
\dot{M}_1 &= r(1 - \frac{N_1 + M_1}{K_1}) M_1 - dM_1 + (d + m_M \tilde{K}) M_2 \\
\dot{M}_2 &= r(1 - \frac{N_2 + M_2}{K_2}) M_2 + dM_1 - (d + m_M \tilde{K}) M_2
\end{align*}
\]

We linearize about the equilibrium $(K_1, K_2, 0, 0)$ which occurs when $m_R = m^*$. Since we wish to examine the stability of this equilibrium for a mutant playing a nearby strategy, we set $m_M = m^* + \epsilon$ where $|\epsilon| << 1$. Note that we can simplify both $m_R \tilde{K}$ and $m_M \tilde{K}$ using the identity $m^* = d(1 + \frac{K_1}{K_2})$. Then, $m_R \tilde{K} = d(\frac{K_1}{K_2} - 1)$, $m_M \tilde{K} = d(\frac{K_1}{K_2} - 1) + \epsilon \tilde{K}$. We shift the equilibrium to the origin using the substitution

\[
\begin{align*}
x_1 &= N_1 - K_1 \\
x_2 &= N_2 - K_2 \\
y_1 &= M_1 \\
y_2 &= M_2
\end{align*}
\]
which leads to the system

\[
\begin{align*}
\dot{x}_1 &= -\frac{r}{K_1}(x_1 + y_1)(x_1 + K_1) - d(x_1 - \frac{K_1}{K_2}x_2) \\
\dot{x}_2 &= -\frac{r}{K_2}(x_2 + y_2)(x_2 + K_2) + d(x_1 - \frac{K_1}{K_2}x_2) \\
\dot{y}_1 &= -\frac{r}{K_1}(x_1 + y_1)y_1 - d(y_1 - \frac{K_1}{K_2}y_2) + \epsilon \tilde{K}y_2 \\
\dot{y}_2 &= -\frac{r}{K_2}(x_2 + y_2)y_2 + d(y_1 - \frac{K_1}{K_2}y_2) - \epsilon \tilde{K}y_2
\end{align*}
\]

Now, we make the following change of variables

\[
\begin{align*}
X_1 &= K_2x_1, \quad X_2 = K_1x_2, \\
Y_1 &= K_2y_1, \quad Y_2 = K_1y_2, \\
\tau &= rt
\end{align*}
\]

which leads to the equivalent system

\[
\begin{align*}
\dot{X}_1 &= -\frac{1}{K_1K_2}(X_1 + Y_1)(X_1 + K_1K_2) - \frac{d}{r}(X_1 - X_2) \\
\dot{X}_2 &= -\frac{1}{K_1K_2}(X_2 + Y_2)(X_2 + K_1K_2) + \frac{dK_1}{rK_2}(X_1 - X_2) \\
\dot{Y}_1 &= -\frac{1}{K_1K_2}(X_1 + Y_1)Y_1 - \frac{d}{r}(Y_1 - Y_2) + \epsilon \tilde{K}K_2Y_2 \\
\dot{Y}_2 &= -\frac{1}{K_1K_2}(X_2 + Y_2)Y_2 + \frac{dK_1}{rK_2}(Y_1 - Y_2) - \epsilon \tilde{K}Y_2
\end{align*}
\]

To diagonalize this system, we first find its eigenvalues and eigenvectors. We evaluate the Jacobian of this system about the equilibrium at the origin

\[
J = \begin{bmatrix}
-1 - \frac{d}{r} & \frac{d}{r} & -1 & 0 \\
\frac{dK_1}{rK_2} & -1 - \frac{dK_2}{rK_2} & 0 & -1 \\
0 & 0 & \frac{d}{r} + \epsilon \tilde{K} \frac{K_2}{K_1} & 0 \\
0 & 0 & \frac{dK_1}{rK_2} & -\frac{dK_2}{rK_2} - \epsilon \tilde{K} \frac{r}{K_2}
\end{bmatrix}
\]
We can solve for the eigenvalues and eigenvectors of this system yielding

\[
P = \begin{bmatrix}
\frac{-d K_1 (K_1+K_2)^2 + K_2^2 (-K_1+K_2) r e - d K_1 K_2 (K_2 (r - e) + K_1 (r + e))}{d K_1 (K_1+K_2) (d (K_1+K_2) + r K_2)} & 1 & \frac{r (K_1 K_2 + K_2^2)}{K_1 (r (K_1+K_2) - e (K_2 K_1 - K_2))} & K_2 \\
\frac{-d K_1^2 + 2 d K_1 K_2 + d K_2^2 + r K_2 (K_1 + K_2) + e K_2 (K_1 - K_2)}{(K_1+K_2) (d (K_1+K_2) + r K_2)} & 1 & - \frac{r (K_1 + K_2)}{r (K_1+K_2) - e (K_1 - K_2)} & 1 \\
\frac{-d K_1^2 - d K_1 K_2 - e K_2 (K_1 - K_2)}{d K_1 (K_1+K_2)} & 0 & - \frac{K_2}{K_1} & 0 \\
1 & 0 & 1 & 0
\end{bmatrix}
\]

(C.04)

with

\[
\Lambda = \begin{bmatrix}
0 & 0 & 0 & 0 \\
0 & -1 & 0 & 0 \\
0 & 0 & - \frac{d}{r} (1 + \frac{K_1}{K_2}) - \epsilon \frac{K_1}{r} & 0 \\
0 & 0 & 0 & -1 - \frac{d}{r} (1 + \frac{K_1}{K_2})
\end{bmatrix}
\]

(C.05)

where \( P \) is the matrix of eigenvectors of \( J \) and \( \Lambda = \text{diag}(\lambda_1, \lambda_2, \lambda_3, \lambda_4) \) contains the eigenvalues of \( J \). Representing (C.02) as \( \dot{X} = JX + f(X) \), multiplying on the left by \( P^{-1} \), and letting \( U = P^{-1} X \), we now have that the first coordinate of \( U = P^{-1} X \), that is \( u_1 \), is tangent to the local center manifold. In other words \( \dot{u}_1 = 0 + \tilde{f}_1(u_1, u_2, u_3, u_4) \) where \( \tilde{f}_1 \) contains the nonlinear terms of the first component of \( P^{-1} X \). We can approximate the dynamics of \( U \) nearby the equilibrium by letting

\[
\begin{align*}
 u_2 &= \alpha_2 u_1^2 \\
 u_3 &= \alpha_3 u_1^2 \\
 u_4 &= \alpha_4 u_1^2
\end{align*}
\]

(C.06a)  (C.06b)  (C.06c)

Differentiating (C.06), comparing it to \( \dot{U} \) and matching coefficients, we can solve for the \( \alpha_i \). Plugging these into the equation for \( \dot{u}_1 \) yields

\[
\dot{u}_1 = -\epsilon^2 \frac{1}{108 d K_2 (3d + r) K_2} u_1^2 + O(u_1^3)
\]

(C.07)

Thus, up to third order, \( \dot{u}_1 < 0 \), so the resident-only equilibrium is locally asymptotically stable.
Proof of Lemma 2. Let $|\mathbf{J}_2|$ and $tr(\mathbf{J}_2)$ represent the determinant and trace, respectively, of $\mathbf{J}_2$, (3.14) in the text, section 3.4. Recall that for a $2 \times 2$ matrix, $|\mathbf{J}_2| = \lambda^{(1)} \cdot \lambda^{(2)}$ and $tr(\mathbf{J}_2) = \lambda^{(1)} + \lambda^{(2)}$ (e.g., Strang, 1976, pg. 179). Let $m_M = m_R$ and $\tau_M = \tau_R$. Then, $|\mathbf{J}_2| = 0$, where the last step follows from (3.9).

$$
|\mathbf{J}_2| = [r(1 - \frac{N_1^*}{K_1}) - d][r(1 - \frac{N_2^*}{K_2}) + r(1 - \frac{N_1^*}{K_1})][-d - m_R(\tau_R \tilde{N} + (1 - \tau_R) \tilde{K})]
$$

$$
= -dr(1 - \frac{N_2^*}{K_2}) + r(1 - \frac{N_1^*}{K_1})[r(1 - \frac{N_2^*}{K_2}) - d - m_R(\tau_R \tilde{N} + (1 - \tau_R) \tilde{K})]
$$

$$
= -dr(1 - \frac{N_2^*}{K_2}) - r(1 - \frac{N_1^*}{K_1})d \frac{N_1^*}{N_2^*}
$$

$$
= -\frac{d}{N_2^*} [(r(1 - \frac{N_2^*}{K_2})N_2^* + r(1 - \frac{N_1^*}{K_1})N_1^*)]
$$

$$
= 0
$$

$$
tr(\mathbf{J}_2) = [r(1 - \frac{N_1^*}{K_1}) - d] + [r(1 - \frac{N_2^*}{K_2}) - d - m_M(\tau_M \tilde{N} + (1 - \tau_M) \tilde{K})]
$$

$$
= -(d + m_R(\tau_R \tilde{N} + (1 - \tau_R) \tilde{K})) \frac{N_2^*}{N_2^*} - d \frac{N_1^*}{N_2^*}
$$

$$
< 0
$$

Therefore, $\lambda^{(1)} = 0$ and $\lambda^{(2)} < 0$. 

Proof of Lemma 3. First, assume $\tilde{N} > 0$. Then, $\frac{N_2^*}{K_2} > \frac{N_1^*}{K_1}$. Since $M_i^* = 0$, the sum of equations
(3.6) equals equation (3.9), so consider (3.9).

\[
0 = r(1 - \frac{N_1^*}{K_1})N_1^* + r(1 - \frac{N_2^*}{K_2})N_2^*
\]

\[
\Rightarrow 0 = (1 - \frac{N_1^*}{K_1}) + (1 - \frac{N_2^*}{K_2})\frac{N_2^*}{N_1^*}
\]

\[
> (1 - \frac{N_2^*}{K_2}) + (1 - \frac{N_2^*}{K_2})\frac{N_2^*}{N_1^*}
\]

\[
= (1 - \frac{N_2^*}{K_2})(1 + \frac{N_2^*}{N_1^*})
\]

\[
\Rightarrow N_2^* > K_2.
\]

The case for $\tilde{N} < 0$ proceeds analogously. □

**Proof of Lemma 4.** We prove this by contradiction. Fix $\tau_R = \tau^*$. When $m_R = m^*$ and $\tau_R = \tau^*$, $\tilde{N} = 0$ at equilibrium. Assume $m_R < m^*$ and $\tilde{N} < 0$. Then, by lemma 3, $N_1^* > K_1$ and $N_2^* < K_2$.

Consider (3.6b) at equilibrium.

\[
\dot{N}_2 = 0 = r(1 - \frac{N_2^*}{K_2})N_2^* + d(N_1^* - N_2^*) - m_R(1 - \tau^*)\tilde{K}N_2^* - m_R\tau^*\tilde{K}N_1^*
\]

\[
> r(1 - \frac{N_2^*}{K_2})N_2^* + d(N_1^* - N_2^*) - m^*(1 - \tau^*)\tilde{K}N_2^* - m_R\tau^*\tilde{K}N_1^*
\]

\[
= r(1 - \frac{N_2^*}{K_2})N_2^* + d(N_1^* - N_2^*) - d\frac{K_1}{K_2}N_2^* - m_R\tau^*\tilde{K}N_1^*
\]

\[
> r(1 - \frac{N_2^*}{K_2})N_2^* + d(N_1^* - N_2^*) - d(K_1 - K_2) - m_R\tau^*\tilde{K}N_1^*
\]

\[
= r(1 - \frac{N_2^*}{K_2})N_2^* + d(N_1^* - K_1 + K_2 - N_2^*) - m_R\tau^*\tilde{K}N_1^*
\]

\[
> 0
\]

where in the third line we use (3.5) and the identity $m^*(1 - \tau^*)\tilde{K} = d\frac{K_1}{K_2} - 1)$. Thus, by contradiction, $m_R < m^* \Rightarrow \tilde{N} > 0$. The case for $\tilde{N} < 0$ proceeds analogously. □

**Proof of Lemma 5.** First, recall that $|J_2| = \lambda^{(1)} \cdot \lambda^{(2)}$, and by lemma 2, $\lambda^{(1)} = 0$ and $\lambda^{(2)} < 0$ when $m_R = m_M = m$ and $\tau_R = \tau_M = \tau$. 
Assume $m > m^\ast$. By lemma 4, when $m < m^\ast$, we have $\tilde{N} > 0$. Then,

$$\frac{\partial |J_2|}{\partial m_M} = \frac{\partial \lambda^{(1)}}{\partial m_M} \cdot \lambda^{(2)},$$

but by direct calculation

$$\frac{\partial |J_2|}{\partial m_M} = r(1 - \frac{N_1^\ast}{K_1})[-(\tau^\ast \tilde{N} + (1 - \tau^\ast)\tilde{K})]. \tag{D.01}$$

By lemma 3, $N_1^\ast < K_1$, thus (D.01) is negative. An application of lemma 2 yields $\frac{\partial \lambda^{(1)}}{\partial m_M} > 0$.

Now, assume $m > m^\ast$. Then, $\tilde{N} < 0$, and

$$\frac{\partial |J_2|}{\partial m_M} = \frac{\partial \lambda^{(1)}}{\partial m_M} \cdot \lambda^{(2)},$$

but by direct calculation

$$\frac{\partial |J_2|}{\partial m_M} = \tilde{N}r(1 - \frac{N_2^\ast}{K_2}) - (1 - \tau)\tilde{K}r(1 - \frac{N_1^\ast}{K_1})$$

$$= r(1 - \frac{N_2^\ast}{K_2})[\frac{N_2^\ast}{N_1^\ast}(1 - \tau)\tilde{K} + \tau \tilde{N}]. \tag{D.02}$$

Nearby $(N_1, N_2) = (K_1, K_2)$, we can choose $N_1^\ast$ and $N_2^\ast$ so that $\frac{N_2^\ast}{N_1^\ast}(1 - \tau)\tilde{K} + \tau \tilde{N} > 0$ as long as $\tau \neq 1$ ($\tau = 1$ is ruled out below). By lemma 3, $N_2^\ast < K_2$, so (D.02) is positive. An application of lemma 2 yields $\frac{\partial \lambda^{(1)}}{\partial m_M} < 0$.

Note that when $\tau = 1$ and $\tilde{N} < 0$, equation (3.6b) at equilibrium becomes

$$0 = r(1 - \frac{N_2^\ast}{K_2})N_2^\ast + d(N_1^\ast - N_2^\ast) - m\tilde{N}N_1^\ast$$

$$> r(1 - \frac{N_2^\ast}{K_2})N_2^\ast - m\tilde{N}N_1^\ast$$

$$\geq 0$$

Thus, when $\tau = 1$, $\tilde{N} \geq 0$, by contradiction. Therefore, $\tau \neq 1$. \qed

Proof of Lemma 6. For a fixed $m^\ast$, $(m^\ast, \tau)$ lies above the optimal $m^\ast$, $\tau^\ast$ curve when $\tau < \tau^\ast$. This can also be worded: for a fixed $\tau^\ast$, $(m, \tau^\ast)$ lies above the optimal $m^\ast$, $\tau^\ast$ curve when $m > m^\ast$. 
Then, by lemma 4, it is clear that $\tilde{N} < 0$ when $\tau < \tau^*$. Then,

$$\frac{\partial |J_2|}{\partial \tau_M} = \frac{\partial \lambda^{(1)}}{\partial \tau_M} \cdot \lambda^{(2)},$$

but by direct calculation

$$= m_M[Kr(1 - \frac{N_1^*}{K_1}) + \tilde{N}r(1 - \frac{N_2^*}{K_2})]. \tag{D.03}$$

By lemma 3, $N_1^* > K_1$ and $N_2^* < K_2$. Therefore, (D.03) is negative and an application of lemma 2 yields $\frac{\partial \lambda^{(1)}}{\partial \tau_M} > 0$.

Now assume that $\tau > \tau^*$ (hence $\tilde{N} > 0$). Then,

$$\frac{\partial |J_2|}{\partial \tau_M} = \frac{\partial \lambda^{(1)}}{\partial \tau_M} \cdot \lambda^{(2)},$$

but by direct calculation

$$= -m_M[\tilde{N} - \tilde{K}][r(1 - \frac{N_1^*}{K_1})]. \tag{D.04}$$

By lemma 3, $N_1^* < K_1$ and $N_2^* > K_2$. Thus, the sign of (D.04) depends on the sign of $\tilde{N} - \tilde{K}$.

First, we prove that $N_2^* \leq N_1^*$. Then, we show that this implies that $\tilde{N} - \tilde{K} \leq 0$.

We can easily prove, by contradiction, that $N_2^* < N_1^*$ (cf. Holt, 1985). Assume $N_2^* \geq N_1^*$. By assumption, $\tilde{N} > 0$, thus by lemma 3, $N_2^* > K_2$. By equation (3.3b),

$$0 = \dot{\tilde{N}} = r(1 - \frac{N_2^*}{K_2})N_2^* + d(N_1^* - N_2^*) - m(\tilde{N} + (1 - \tau)\tilde{K})N_2^*$$

$$\leq [r(1 - \frac{N_2^*}{K_2}) - m(\tilde{N} + (1 - \tau)\tilde{K})]N_2^*$$

$$< -m(\tilde{N} + (1 - \tau)\tilde{K})N_2^*$$

$$< 0$$

Therefore, by contradiction, $N_2^* < N_1^*$, and we can now determine the sign of $\tilde{N} - \tilde{K}$.
\[
[\tilde{N} - \tilde{K}] = \left[ \frac{N_2^* - N_1^*}{K_2} - \frac{K_1 - K_2}{K_1 + K_2} \right]
= \left[ \frac{1}{(N_2^*/K_2 + N_1^*/K_1)(K_1 + K_2)} \left( \frac{N_2^*}{K_2} - \frac{N_1^*}{K_1} \right) \left( K_1 + K_2 \right) - \left( K_1 - K_2 \right) \left( \frac{N_2^*}{K_2} + \frac{N_1^*}{K_1} \right) \right]
\leq 0
\]

Therefore, (D.04) is positive and an application of lemma 2 yields \( \frac{\partial \lambda^{(1)}}{\partial \tau M} < 0 \).

Here, we present a proof of convergence stability using the stability criteria (2.4) and (2.5) from chapter 2. Our dynamical system is given by (3.6) from chapter 3 when \( k = 0 \). The mutant’s ability to increase when rare is given by the lower right \( 2 \times 2 \) matrix \( J_2 \) of the Jacobian of (2.2) evaluated at \( (N_1^*, N_2^*, 0, 0) \),

\[
J_2 = \begin{bmatrix}
    r(1 - \frac{N_1^*}{K_1}) - (d + m_M \tau M \max(0, -\tilde{N})) & d + m_M [\tau M \max(0, \tilde{N}) + (1 - \tau M) \tilde{K}]
    \\
    d + m_M \tau M \max(0, -\tilde{N}) & r(1 - \frac{N_2^*}{K_2}) - (d + m_M [\tau M \max(0, \tilde{N}) + (1 - \tau M) \tilde{K}])
\end{bmatrix}
\]

Refer to the text in chapter 3, equation (3.13), for a detailed explanation. We assign \( \lambda^{(1)} \) to be the largest eigenvalue of \( J_2 \) and and \( \lambda^{(2)} \) to be the other eigenvalue of that matrix. Recall from the text that \( \lambda^{(1)} \) is the mutant’s growth rate when rare – in other words, \( \lambda^{(1)} \) and \( F \) (from the text, (2.4) and (2.5)) represent the same quantity.

**Theorem 7.** The information-use strategy given by (2.3a) in chapter 2 (also (3.5) in chapter 3) is convergence stable if one considers mutations in only one of the strategy components \( m \) or \( \tau \) at a single time.

**Proof.** The proof is elementary. The failure to prove convergence when mutations can occur in both \( m \) and \( \tau \) at the same time is due to the quantity \( F_{mm} F_{\tau \tau} - F_{m\tau} F_{\tau m} = 0 \), which reflects that all strategies along the ESSet are equivalent, as explained in section 3.6. Thus, the stability condition (2.5) does not hold.
To show that the first stability condition (2.4) holds, we must assume that \( g_{m,\tau} < \min(g_{m,m}, g_{\tau,\tau}) \).

For convenience, we make the following representations

\[
D_1 := \frac{r K_2 \hat{K}^2}{K_1(r + 2d + m(\tau \frac{K_1 + K_2}{2K_1} + (1 - \tau) \hat{K}))} > 0
\]

\[
D_2 := \frac{r K_2 \hat{K}^2}{K_1(r + 2d + m(\tau \frac{K_1 + K_2}{2K_2} + (1 - \tau) \hat{K}))} > 0
\]

Then,

\[
F_{mm} g_{m,m} + (F_{m} + F_{m\tau}) g_{m,\tau} + F_{\tau\tau} g_{\tau,\tau} = (\lambda^{(2)} (1 - \tau)^2 D_i g_{m,m} + (-m(1 - \tau) D_i - m(1 - \tau) D_i) g_{m,\tau} + m^2 D_i g_{\tau,\tau})
\]

\[
= \lambda^{(2)} (1 - \tau)^2 D_i g_{m,m} + m^2 D_i g_{\tau,\tau}
\]

\[
< \lambda^{(2)} (m - (1 - \tau))^2 \cdot \max(g_{m,m}, g_{\tau,\tau})
\]

\[
< 0
\]

where when \( \tilde{N} \geq 0 \), we assign \( D_i = D_1 \) and when \( \tilde{N} \leq 0 \), we assign \( D_i = D_2 \). On line (D.06d), we have used the assumption that \( g_{m,\tau} < \min(g_{m,m}, g_{\tau,\tau}) \).

Now we show that the inequality (2.5) does not hold.

\[
F_{mm} F_{\tau\tau} - F_{m\tau} F_{\tau m} = (\lambda^{(2)})^2 [(1 - \tau)^2 D_i \cdot m^2 D_i - (-m(1 - \tau) D_i)(-m(1 - \tau) D_i)]
\]

\[
= (\lambda^{(2)} D_i)^2 [(1 - \tau)^2 m^2 - m^2(1 - \tau)^2]
\]

\[
= 0
\]

Thus, the second stability condition cannot be met.

To show that the strategy is convergence stable if we allow mutations in \( m \) or \( \tau \) (we are now ruling out a simultaneous \( m \) and \( \tau \) mutation), we need to show that condition (1.5b) from chapter 1 holds. In terms of our current notation, we need to show that

\[
\frac{\partial^2 \lambda^{(1)}}{\partial m_R \partial m_M} + \frac{\partial^2 \lambda^{(1)}}{\partial m^2_M} < 0,
\]

(D.07)

and the same for \( \tau_M \) and \( \tau_R \).
We can directly calculate the quantities in Table D.01 from (D.05). The partial derivatives \( \frac{\partial N^*_1}{\partial m_R} \) and \( \frac{\partial N^*_1}{\partial \tau_R} \) depend on the derivatives of \( \tilde{N} \) with respect to \( m_R \) and \( \tau_R \) as well as the sign of \( \tilde{N} \) at equilibrium. Direct calculation yields

\[
\frac{\partial \tilde{N}}{\partial m_R} = -\frac{\partial N_1}{\partial m_R} K_1 + K_2 \quad (D.08a)
\]

\[
\frac{\partial \tilde{N}}{\partial \tau_R} = -\frac{\partial N_1}{\partial \tau_R} K_1 + K_2 \quad (D.08b)
\]

and, using (D.08), we find that when \( \tilde{N} \geq 0 \)

\[
\frac{\partial N^*_1}{\partial m_R} = -\frac{\partial N^*_2}{\partial m_R} = \frac{(1 - \tau)\tilde{K} K_2}{r + 2d + m(\tau \frac{K_1 + K_2}{2K_1} + (1 - \tau)\tilde{K})} \quad (D.09a)
\]

\[
\frac{\partial N^*_1}{\partial \tau_R} = -\frac{\partial N^*_2}{\partial \tau_R} = -\frac{m\tilde{K} K_2}{r + 2d + m(\tau \frac{K_1 + K_2}{2K_1} + (1 - \tau)\tilde{K})} \quad (D.09b)
\]

whereas when \( \tilde{N} \leq 0 \)

\[
\frac{\partial N^*_1}{\partial m_R} = -\frac{\partial N^*_2}{\partial m_R} = \frac{(1 - \tau)\tilde{K} K_2}{r + 2d + m(\tau \frac{K_1 + K_2}{2K_2} + (1 - \tau)\tilde{K})} \quad (D.010a)
\]

\[
\frac{\partial N^*_1}{\partial \tau_R} = -\frac{\partial N^*_2}{\partial \tau_R} = -\frac{m\tilde{K} K_2}{r + 2d + m(\tau \frac{K_1 + K_2}{2K_2} + (1 - \tau)\tilde{K})} \quad (D.010b)
\]

We can calculate the necessary derivatives of \( \lambda^{(1)} \) to show that (D.07) will hold by using the
Derivative Value when \( N \geq 0 \) Value when \( N \leq 0 \)
\[
\frac{\partial^2 \lambda^{(1)}}{\partial m_M \partial m_R} = 0 \quad 0
\]
\[
\frac{\partial^2 \lambda^{(1)}}{\partial m_M \partial \tau_R} = \frac{r((1-\tau)K)^2K_2}{K_1(r + 2d + m(\tau \frac{K_1 + K_2}{2K_1} + (1-\tau)K))} \lambda^{(2)} \quad \frac{r((1-\tau)K)^2K_2}{K_1(r + 2d + m(\tau \frac{K_1 + K_2}{2K_1} + (1-\tau)K))} \lambda^{(2)}
\]
\[
\frac{\partial^2 \lambda^{(1)}}{\partial m_M \partial \tau_M} = \frac{rm(1-\tau)K^2K_2}{K_1(r + 2d + m(\tau \frac{K_1 + K_2}{2K_1} + (1-\tau)K))} \lambda^{(2)} \quad \frac{rm(1-\tau)K^2K_2}{K_1(r + 2d + m(\tau \frac{K_1 + K_2}{2K_1} + (1-\tau)K))} \lambda^{(2)}
\]
\[
\frac{\partial^2 \lambda^{(1)}}{\partial \tau_M \partial m_R} = \frac{K_1(r + 2d + m(\tau \frac{K_1 + K_2}{2K_1} + (1-\tau)K)) - rm(1-\tau)K^2K_2}{K_1(r + 2d + m(\tau \frac{K_1 + K_2}{2K_1} + (1-\tau)K))} \lambda^{(2)} \quad \frac{K_1(r + 2d + m(\tau \frac{K_1 + K_2}{2K_1} + (1-\tau)K)) - rm(1-\tau)K^2K_2}{K_1(r + 2d + m(\tau \frac{K_1 + K_2}{2K_1} + (1-\tau)K))} \lambda^{(2)}
\]

Table D.02: Partial derivatives of the mutant’s growth rate (fitness) when rare.

values from table D.01. Recall that \(|J_2| = \lambda^{(1)} \cdot \lambda^{(2)}\).

\[
\frac{\partial^2 |J_2|}{\partial x \partial y} = \frac{\partial^2}{\partial x \partial y} \left[ \lambda^{(1)} \cdot \lambda^{(2)} \right] = \lambda^{(2)} \frac{\partial^2 \lambda^{(1)}}{\partial x \partial y} + \frac{\partial \lambda^{(1)}}{\partial x} \frac{\partial \lambda^{(2)}}{\partial y} + \frac{\partial \lambda^{(1)}}{\partial y} \frac{\partial \lambda^{(2)}}{\partial x} + \lambda^{(1)} \frac{\partial^2 \lambda^{(2)}}{\partial x \partial y} \quad (D.011)
\]

where \( x \) and \( y \) can be \( m_R, m_M, \tau_R, \tau_M \). We evaluate the derivatives where \( m_M = m_R = m^* \) and \( \tau_M = \tau_R = \tau^* \), so the first order partial derivatives are zero and \( \lambda^{(1)} = 0 \). Therefore, (D.011) becomes

\[
\frac{\partial^2 |J_2|}{\partial x \partial y} = \lambda^{(2)} \frac{\partial^2 \lambda^{(1)}}{\partial x \partial y} \quad (D.012)
\]

Using (D.012) and the values in table D.01, we calculate the necessary derivatives and list them in table D.02. Recall from lemma 2 that \( \lambda^{(2)} < 0 \). Then, the necessary conditions for convergence stability (D.07) hold immediately from table D.02. \( \square \)