

AN ABSTRACT OF THE DISSERTATION OF

Haley A. Ohms for the degree of Doctor of Philosophy in Integrative Biology
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Abstract approved: _____

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Natural selection, in its most basic form, is described as a process in which traits increase or decrease in frequency depending on their fitness, and only the trait with the highest fitness will remain in the population. Yet, populations rarely have a single ‘optimal’ trait. The way natural selection maintains this observed variation within populations has been a keen focus of evolutionary biologists. In the following chapters, I focus on how natural selection maintains a form of phenotypic variation referred to as ‘partial migration’. Partial migration is the coexistence of migratory and non-migratory phenotypes, and is found in a wide variety of taxa. I find that some, but not all forms of density-dependent competition can lead to the evolution and maintenance of partial migration (i.e., partial migration as an evolutionarily stable strategy (ESS) and convergent stable strategy (CSS)). Whether density-dependent competition allows for partial migration as an ESS and a CSS depends on how it influences the relative fitnesses of the phenotypes. If compe-

tition changes the relative fitnesses in opposing directions, then it will allow for partial migration. If it affects the relative fitnesses in the same direction, it will not. I then apply these results to a fish species of conservation and commercial concern: *Oncorhynchus mykiss*, or steelhead and rainbow trout. I demonstrate how female steelhead and rainbow trout competing separately for spawning habitat can still be subject to frequency-dependent selection and how this allows for partial migration. The frequency-dependent selection also results in strong feedbacks between survival and reproduction, which produces a non-linear response in the migration propensity ESS and CSS. In practical terms, this means that conservation or management actions may not affect the population as expected, and measuring the propensity for migration in wild populations is notoriously difficult. To address this difficulty, I develop a method to measure the propensity for migration in wild populations that can be used to test the predicts I generated in the two previous chapters. The method is called sex-ratio balancing and it relies on a fundamental relationship between sex ratios and the propensity for migration. Sex ratios are much easier to measure than the propensity for migration and the ease of measurement makes this method valuable for studying many different partially migratory taxa.

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The Evolutionary Stability of Partial Migration

by

Haley A. Ohms

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APPROVED:

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Chair of the Department of Integrative Biology

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Haley A. Ohms, Author

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As someone who arrived in Corvallis seven years ago with plans to study ‘fish’, I smile to think that I am now receiving a PhD from a ‘bug’ lab, with a dissertation on evolutionary theory. It has been quite the journey.

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CONTRIBUTION OF AUTHORS

Patrick De Leenheer and Anushaya Mohapatra contributed the mathematical analysis and proofs in Chapter 2 and Appendix A. This includes the analysis starting at equation 2.7 and continuing through the adaptive dynamics and to the resulting equations 2.13-2.15. It also includes all proofs in Appendix A.

Dave Lytle, Alix Gitelman, and Chris Jordan made significant contributions to the sex-ratio balancing equation (equation 4.2) and concept. Alix Gitelman contributed the Bayesian highest posterior density interval derivation and simulation code in Section 4.3.1.

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Chapter 1 Introduction

At the center of evolutionary theory lies the idea of natural selection, in which traits increase or decrease in frequency depending on their fitness, and only the trait with the highest fitness will remain in the population. Despite this central idea, there are many examples where multiple trait values coexist within populations, even when they have different fitnesses. These are referred to by many names, including ‘dimorphisms’, ‘polyphenisms’, ‘discrete alternative phenotypes’, and ‘alternative tactics’ (Gross 1996; Roff 2002; Stearns 1992), and they come in a variety of forms. For example, some individuals have spines (Harvell 1984) or wings (Crespi 1986) while other individuals within these groups do not. Some fight to attract mates while others sneak for mates (Gross 1996). In perhaps the most dramatic case, some may migrate while others do not (Chapman et al. 2011; Johnson and Gaines 1990; Lundberg 1988). The coexistence of migrants and non-migrants is known, perhaps somewhat misleadingly, as partial migration (Chapman et al. 2011; Lack 1944). The ‘partial’ refers to the population and not the individual behavior. Partial migration has been documented in a wide variety of taxa, from birds to fish, as well as insects, mammals, amphibians, and reptiles (Table 2.1).

There are three main hypotheses for how natural selection leads to partial migration, and phenotypic diversity in general. One is that environmental variation causes parents to ‘spread the risk’, or hedge their bets’, by producing both migrant

and non-migrant offspring because migrants will have higher fitness in some years and non-migrants will have higher fitness in others (den Boer 1968; Gillespie 1974; Slatkin 1974). A second hypothesis is that the fitness of each phenotype is greatest when it is rare (i.e., at low frequency), and as such, balancing selection leads to the mixture of phenotypes where their fitnesses are equal (Charnov 1993; Gromko 1977; Kaitala et al. 1993; Lundberg 1987). This is generally referred to as ‘frequency-dependent selection’, although it can arise through density-dependent competition (Heino et al. 1998; Kokko 2007, 2011). A third hypothesis considers the effect of individual variation, and proposes that an individual’s fitness depends on their condition. Individuals adopt a phenotype based on what will maximize their fitness given their condition. This is often referred to as a ‘conditional strategy’ (Gross 1996; Lundberg 1988) and is maintained by natural selection via the environmental threshold model (Hazel et al. 2004).

Of the three hypotheses, the conditional strategy has received the most attention because there is considerable empirical data showing that migratory tendency is influenced by individual condition and that one phenotype has higher fitness than the other (Adriaensen and Dhondt 1990; Gillis et al. 2008; Grayson and McLeod 2009; Ogonowski and Conway 2009; Olsson et al. 2006; Paez et al. 2011; Skov et al. 2010). The frequency-dependent selection hypothesis has fallen out of favor because there is little empirical evidence that the average fitness of migratory and non-migratory phenotypes are equal (Chapman et al. 2011). Yet, there are two reasons frequency-dependent selection may still be important. Density-dependent competition is commonly observed, and there is evidence that it can

lead to frequency-dependent selection. Kokko (2007, 2011) has shown this theoretically for the prior residence effect, Berejikian et al. (2010) measured it empirically in sneaker/fighter male salmon, as did Dijkstra et al. (2009) in red and blue color morphs of a Lake Victoria cichlid. Additionally, the conditional strategy cannot maintain partial migration alone if there are occasions when the less fit phenotype is more fit than the other (i.e., which phenotype has the higher fitness depends on the circumstances). Under these circumstances frequency-dependent selection is the most likely mechanism for maintaining partial migration (Repka and Gross 1995). Therefore, frequency-dependent selection may be occurring through density-dependent competition or may be playing an under appreciated role in the conditional strategy, and it warrants further research.

My dissertation focuses on how density-dependent competition can lead to frequency-dependent selection, thereby providing a mechanism by which natural selection leads to and maintains partial migration. In the second chapter, I investigate how different forms of density-dependent competition during reproduction can lead to the evolution and maintenance of partial migration. I identify four forms of density-dependent competition that occur during reproduction and use adaptive dynamics to derive equations for the predicted convergent stable strategy (CSS) and an evolutionarily stable strategy (ESS). I find that not all forms of competition lead to partial migration as a CSS and ESS and there are certain conditions that are important. I also find that this system leads to feedbacks with unexpected consequences.

In the third chapter, I apply the results from one of the forms of density-

dependent competition to a fish species of commercial and conservation importance. Steelhead is the migrant form, and rainbow trout is the non-migrant form of the species *Oncorhynchus mykiss*. I use simulations to show how density-dependent competition leads to frequency dependent fitness in this species, and use the ESS and CSS equation from the first chapter to predict how the migration propensity may respond to changes in survival and reproduction.

In the fourth chapter, I propose a method for testing the predictions I made in the two previous chapters. Many of the assumptions and predictions I make require measuring migration propensity, but this is a very difficult thing to measure. I present a new method, which relies on measuring sex ratios in the migrants and residents, and which we refer to as ‘sex-ratio balancing’. Other methods require estimating the number of migrants and non-migrants, which can be challenging at best and impossible at worst. sex-ratio balancing uses sex ratio data that is easy to collect and can be collected in a wide variety of species. This method has the potential to provide important information to the study of partial migration and to generate empirical data to test predictions of the first two chapters.

Chapter 2 The Evolutionary Stability of Partial Migration Under Different Forms of Density-Dependent Competition

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2.1 Introduction

The ways in which phenotypic variation is maintained in populations has been a long standing question in the field of evolutionary ecology (Fisher 1930). An excellent system to investigate the evolution and maintenance of phenotypic variation is partial migration, which is the coexistence of migrant and non-migrant phenotypes within a single population (Lack 1944; Lundberg 1987). Although most theoretical investigations of partial migration have focused on birds (e.g, Kaitala et al. 1993; Kokko 2007; Lundberg 1987, 2013), recent work shows it is a wide-spread phenomenon present in bats, mammals, fish, and insects (Table 2.1).

The evolution and maintenance of partial migration occurs by the process of balancing selection, which requires that the fitnesses of both phenotypes are equal (Kokko 2011). The fitnesses of both phenotypes can be equal, despite having vastly different costs and benefits, if fitness depends on the frequency of migration in the

population (Gromko 1977). Fitness depends on the frequency of migration because it determines the local densities of migrants and non-migrants, that in turn determine the amount of density-dependent competition for resources (Kokko 2011). In this way, density-dependent competition can be the basis of frequency-dependent selection and ultimately the mechanism by which natural selection maintains migratory and non-migratory phenotypes (Heino et al. 1998).

Most theoretical work on the evolution and maintenance of partial migration has focused on how fitness equality can occur because of density-dependent competition (Griswold et al. 2010; Kaitala et al. 1993; Kokko 2007, 2011; Lundberg 1987, 2013; Taylor and Norris 2007) Missing from this body of work is the process of evolution itself. Whether the end point of natural selection will be at the point where fitnesses are equal remains untested. There have also been no direct comparisons of different forms of density-dependent competition to see what characteristics of density-dependent competition allow for balancing selection and partial migration. Density-dependent competition could take on many forms, and given the broad diversity of partially migratory species, we would expect it to. Yet, thus far the only form of competition proven to result in balancing selection and partial migration is when phenotypes compete only among their own phenotype (De Leenheer et al. 2017).

To see what characteristics of density-dependent competition allow for balancing selection and partial migration we addressed the following three questions. First, can we identify forms of density-dependent competition that are most common among partially migratory taxa? Second, which forms of density-dependent

competition can lead to the evolution and maintenance of partial migration through balancing selection, and which forms cannot? And, do the forms that lead to partial migration have similar characteristics? Third, how might taxa experiencing different forms of competition respond differently to changes in survival or reproduction, particularly in regards to climate and land use changes?

To answer these questions, we identified four complimentary forms of density-dependent competition that are experienced by partially migratory populations during reproduction, including those that share breeding habitat and those that share only non-breeding habitat (Chapman et al. 2011; Griswold et al. 2010). We focused on competition specifically during reproduction because migratory and non-migratory phenotypes are often indistinguishable as juveniles, and as a result, there are more observations of competition during reproduction.

We assessed which of the four forms lead to the evolution and maintenance of partial migration using adaptive dynamics. Individuals migrate (or not) based on their propensity for migration. This is a probability that ranges from zero to one. The evolution of partial migration occurs if a migration propensity between zero and one is a convergent stable strategy (CSS), and natural selection maintains that migration propensity if it is an evolutionarily stable strategy (ESS). A migration propensity that is both an ESS and a CSS is one of the strongest notions in adaptive dynamics because not only can a strategy resist invasion by mutants (by being an ESS), but the strategy value adopted by the population will also converge to this strategy in the evolutionary process (i.e., by being a CSS; (Diekmann 2004). We derive equations for the ESS and CSS migration propensities and use these

equations to examine how sensitive the ESS and CSS values are to changes in survival and reproduction characteristics (i.e., competition strength and number of gametes). The ESS sensitives are directly relevant to predicting the future adaptations to climate and land use change among partially migratory species.

2.2 Methods

2.2.1 Forms of competition

We searched the literature for records of partially migratory species and competitive interactions they experience during reproduction. We found 58 species divided among birds, reptiles, amphibians, mammals, fishes, and insects (Table 2.1). Data and descriptions of competition during reproduction, as well as other life stages, was quite limited. However, we used what information we found and identified four general forms of density-dependent reproduction during competition (Figure 2.2). The four forms of density-dependent competition are as follows.

1. Within phenotype: migrants compete only with other migrants for a resource and non-migrants compete only with non-migrants for a resource. This form of competition occurs if migrant and non-migrant reproductive habitat differs (i.e., they nest in different habitats), or reproduction occurs at different times (i.e., migrants mate earlier than non-migrants).
2. Between phenotype: migrants and non-migrants compete for the same resource at the same time and neither has an advantage.

3. Prior residence: non-migrants have an advantage over migrants during reproduction. This includes the prior residence effect' (Kokko et al. 2006) in which non-migrants are present on the reproductive habitat first and compete only among themselves for habitat. Migrants arrive later and must compete among themselves as well as with non-migrants. It also includes cases in which non-migrants have a competitive advantage.
4. Migrant advantage: migrants have an advantage over non-migrants during reproduction. This is the opposite of prior residence. Migrant advantage could occur if migrants are more competitive than non-migrants such that they only compete among themselves for a resource, but non-migrants must compete among themselves and the migrants.

We identified species in each of these categories based on descriptions of their mating behavior and resource use (Table 2.1). Generally, comparisons of mating behavior and competition among and between phenotypes was limited, but we were able to find some information.

2.2.2 Population model

To assess how each of these four forms of density-dependent competition does, or does not, lead to the evolution and maintenance of partial migration, we represent a general partially migratory population with a three stage Leslie matrix model.

$$\begin{pmatrix} x_1(t+1) \\ x_M(t+1) \\ x_N(t+1) \end{pmatrix} = \begin{pmatrix} 0 & f_M(z_M(t)) & f_N(z_N(t)) \\ \phi s_M & 0 & 0 \\ (1-\phi)s_N & 0 & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_M(t) \\ x_N(t) \end{pmatrix}, \quad (2.1)$$

where $x_1(t)$, $x_M(t)$ and $x_N(t)$ are abundances of juveniles, migrant adults and non-migrant adults at time t , respectively (Figure 2.1). Both phenotypes contribute to a common pool of juveniles that have a migration propensity of ϕ . Juveniles become migrant with migration propensity ϕ and non-migrant with propensity $1 - \phi$. Juveniles that become migrant survive to reproduction with a probability of s_M , and those that become non-migrant survive with a probability of s_N . Survival to reproduction is not affected by density-dependent competition in this model.

Reproduction is affected by density-dependent competition and is given by a per-capita fertility function specific to each phenotype and form of competition ($f_i(z_i)$ with $i = M$ or N). We use the Beverton-Holt function:

$$f_i(z) = \frac{a_i}{1 + b_i z} \quad (2.2)$$

which is defined for all non-negative z , and parameterized by two positive parameters a_i and b_i . a_i is the number of gametes (i.e., eggs or sperm) in the absence of competition. b_i controls the rate of decline of $f_i(z)$ and is a measure of the intensity of competition. The important characteristics of the Beverton-Holt function are that total fertilities ($z_i f_i(z_i)$) increase with respect to z_i , but per capita

fertilities decrease with respect to z_i , reflecting that increased abundances always have a negative effect on reproduction. Our results and conclusions that follow apply to any fertility functions that meet these characteristics. Other commonly used fertility functions, such as Hassell's function (De Leenheer et al. 2017) and the density dependence used by Kaitala et al. (1993) satisfy these conditions, but Ricker's function does not (De Leenheer et al. 2017), nor do the linear functions used by Kokko (2007) and Taylor and Norris (2007).

We represent the four forms of density-dependent competition mathematically by switching between two possible arguments z_i in each fertility function f_i in matrix 2.1:

$$\text{Within phenotype: } z_M = x_M \text{ and } z_N = x_N \quad (2.3)$$

$$\text{Between phenotype: } z_M = x_M + x_N \text{ and } z_N = x_M + x_N \quad (2.4)$$

$$\text{Prior residence: } z_M = x_M + x_N \text{ and } z_N = x_N \quad (2.5)$$

$$\text{Migrant advantage: } z_M = x_M \text{ and } z_N = x_M + x_N \quad (2.6)$$

We assume that both migrant and non-migrant phenotypes could exist in isolation of one another (i.e., neither is a population sink). And, because of the density dependence fertilities, both phenotypes would reach equilibrium in isolation. As a result, we assume there exist two positive numbers \hat{x}_M and \tilde{x}_N such that

$$s_M f_M(\hat{x}_M) = 1 = s_N f_N(\tilde{x}_N). \quad (2.7)$$

Note that if these numbers exist, they are necessarily unique because the f_i are decreasing.

For each fixed migration propensity ϕ , the behavior of model 2.1, there exists a unique nonzero fixed point $x^*(\phi) = (x_1^*(\phi), x_M^*(\phi), x_N^*(\phi))$ which is globally stable (De Leenheer et al. (2017), Appendix A). Moreover, in case of the extreme migration propensity $\phi = 1$, which means that no offspring will become non-migrant, it follows that

$$x_M^*(1) = \hat{x}_M \text{ and } x_N^*(1) = 0.$$

This shows that \hat{x}_M represents the stable equilibrium abundance of migrants in a population of only migrants. Similarly, when $\phi = 0$, meaning that no offspring become migrants, it follows that $x_M^*(0) = 0$ and $x_N^*(0) = \tilde{x}_N$, and \tilde{x}_N represents the stable equilibrium abundance of non-migrants in a population only only non-migrants.

Notice that when the equilibrium abundances of migrants and non-migrants are positive, their ratio is given by:

$$\frac{x_M^*(\phi)}{x_N^*(\phi)} = \frac{\phi}{1 - \phi} \frac{s_M}{s_N} \frac{x_1(t)}{x_1(t)} \quad (2.8)$$

$x_1(t)$ cancels, and inverting this formula provides us with a way to determine the value of ϕ :

$$\phi = \frac{\frac{s_N}{s_M}}{\frac{x_N^*(\phi)}{x_M^*(\phi)} + \frac{s_N}{s_M}}.$$

In other words, the migration propensity ϕ can be computed quite easily, if (1) the

ratio of the equilibrium abundances of the two types is known, and (2) the ratio of their survival probabilities is known. In particular, no knowledge of the per capita fertilities is required.

Although this is a convenient and a very useful way to determine ϕ , it does not explain why this particular value has been adopted as the migration propensity of the population. We need additional analysis to learn whether this value of ϕ arises from natural selection. For this we use adaptive dynamics. Partial migration is said to occur when the migration propensity ϕ is strictly between zero and one, and is maintained by natural selection as an evolutionarily stable strategy (ESS) and convergent stable strategy (CSS), two central notions featuring in the theory of adaptive dynamics which will be reviewed below. In contrast, when the migration propensity ϕ takes either of its extreme values 0 or 1, and is also maintained as an ESS and a CSS, partial migration does not occur. In these two cases, evolution drives the population toward a purely non-migrant or migrant composition, respectively.

2.2.3 Adaptive dynamics

We use adaptive dynamics (Diekmann 2004) to analyze whether partial migration is an ESS and a CSS under the four forms of density-dependent competition. Adaptive dynamics is a method that allows us to mimic the process of natural selection and see what the end point of natural selection would be. It starts with a ‘resident’ population containing individuals with a ‘resident’ migration propensity

(ϕ). A genetic mutation occurs in one individual that gives it a different migration propensity (ϕ'), which is called the ‘mutant’. Adaptive dynamics determines whether the mutant can successfully invade the resident population and ultimately replace it. A migration propensity is an ESS if it cannot be invaded by mutants with differing migration propensities (De Leenheer et al. 2017; Diekmann 2004), and is denoted by ϕ^* . A migration propensity is a CSS if all mutant invasions near ϕ^* converge toward the ϕ^* and not away from it. It is not always the case that an ESS is a CSS, or vice versa. A migration propensity between zero and one that is both an ESS and a CSS is the strongest theoretical evidence that adaptive dynamics can provide for the evolution of partial migration.

To introduce a mutant phenotype into the resident population defined in equation 3.4, we consider a resident population that uses strategy value ϕ , and assume invasion by a mutant population using strategy value $\phi' \neq \phi$. The resulting dynamical population model takes the following form:

$$X(t + 1) = A(X(t))X(t), \tag{2.9}$$

where

$$X(t) = \begin{pmatrix} \text{resident egg abundance } (x_1(t)) \\ \text{resident migrant adult abundance } (x_M(t)) \\ \text{resident non-migrant adult abundance } (x_N(t)) \\ \text{mutant egg abundance } (y_1(t)) \\ \text{mutant migrant adult abundance } (y_M(t)) \\ \text{mutant non-migrant adult abundance } (y_N(t)) \end{pmatrix},$$

$$A(X(t)) = \begin{pmatrix} A_1(x(t) + y(t), \phi) & 0 \\ 0 & A_1(x(t) + y(t), \phi') \end{pmatrix}$$

with

$$x = \begin{pmatrix} x_1 \\ x_M \\ x_N \end{pmatrix}, \quad y = \begin{pmatrix} y_1 \\ y_M \\ y_N \end{pmatrix},$$

and

$$A_1(x, \phi) = \begin{pmatrix} 0 & f_M(z_M^x(t) + z_M^y(t)) & f_N(z_N^x(t) + z_N^y(t)) \\ \phi s_M & 0 & 0 \\ (1 - \phi) s_N & 0 & 0 \end{pmatrix} \quad (2.10)$$

where (z_M^x, z_N^x) corresponds to one of the four forms of density-dependent competition in the 'resident' population whose abundance vector is x and migration propensity is ϕ . (z_M^y, z_N^y) describes the same scenario but for the 'mutant' popu-

lation whose abundance vector is y and migration propensity is ϕ' .

We assume that the mutant appears as a single individual in the environment occupied by the resident. Thus, the mutant will experience the same form of density dependence as the resident phenotype. We also assume that the resident population is at a stable equilibrium $x^*(\phi)$. Mathematically, we investigate this model's behavior near the fixed point $(x, y) = (x^*(\phi), 0)$. To determine whether the mutant can invade and replace the resident, we determine the mutant's fitness in the environment occupied by the resident. A commonly used fitness measure is the basic reproduction number, denoted as R_0 (Allen and van den Driessche 2008), minus 1. The reason for subtracting one is that it makes fitness positive if the mutant can successfully invade and replace the resident, and negative if it cannot (Diekmann 2004). Linearizing the resident-mutant model (2.9) near the relevant fixed point $(x^*(\phi), 0)$, it can be shown, as in De Leenheer et al. (2017), that fitness, which we denote by $W(\phi, \phi')$, equals:

$$W(\phi, \phi') = (\phi' - \phi) [s_M f_M(z_M^*(\phi)) - s_N f_N(z_N^*(\phi))]$$

where $z_M^*(\phi)$ and $z_N^*(\phi)$ denote the values of z_M and z_N , evaluated at the resident's equilibrium $x^*(\phi)$ described in the Methods section. This formula shows that the sign of the fitness is equal to the product of the sign of $\phi' - \phi$, and the sign of the second factor in the square brackets. In particular, fitness will always be zero if and only if $\phi' = \phi$ or the factor in the square brackets is zero. That fitness is zero when $\phi' = \phi$ is not surprising because in this case the mutant is identical to the

resident. Notice that the factor in the square brackets only depends on ϕ , but not on ϕ' , and thus it is natural to determine those values of ϕ which make this factor zero. Following the same arguments as in De Leenheer et al. (2017), by exploiting that $x^*(\phi)$ is the stable nonzero equilibrium of 2.10 it can be shown that the factor in the square brackets is zero if and only if

$$s_M f_M(z_M^*(\phi)) = 1 = s_N f_N(z_M^*(\phi)),$$

or equivalently, because the fertility functions f_M and f_N are decreasing, when

$$z_M^*(\phi) = \hat{x}_M \tag{2.11}$$

$$z_N^*(\phi) = \tilde{x}_N \tag{2.12}$$

Depending on which of the four possible forms of competition is chosen, we can find the values of ϕ which satisfy these two equations, and which identify when fitness is zero. Once this is achieved, the mathematical analysis performed in Appendix A. enables us to determine the sign of the fitness function $W(\phi, \phi')$ for all possible combinations of resident and mutant migration propensity pairs (ϕ, ϕ') . The results can be visualized with pairwise invasibility plots (PIPs; Figure 2.3). A PIP has the resident migration propensity (ϕ) on the horizontal axis and the mutant migration propensity (ϕ') on the vertical axis. Resident and mutant migration propensities are equal ($\phi = \phi'$) on the diagonal line. Regions where $W(\phi, \phi') > 0$ are labeled with a plus (+) and correspond to cases where mutants have positive fitness and

can successfully 'invade' the resident; regions with $W(\phi, \phi') < 0$ are labeled with a minus (-), and here, mutants have lower fitness and cannot invade the resident.

Whether the migration propensity is an ESS and/or CSS can be determined on the basis of the PIP, as well as on the basis of the nonlinear stability analysis performed in Appendix A. A resident migration propensity (ϕ^*) is an ESS if the vertical line $\phi = \phi^*$ in the PIP is contained in a region where fitness is negative (except on the diagonal where fitness is always zero). Unfortunately, this criterion often fails, and instead we find a candidate ESS value ϕ^* , which corresponds to a vertical line $\phi = \phi^*$ in the PIP where fitness is identically zero, i.e. which is such that $W(\phi^*, \phi') = 0$ for all ϕ' . A candidate ESS is a genuine ESS if $(x^*(\phi^*), 0)$ is a stable fixed point for the resident-mutant model (2.9) for all $\phi' \neq \phi^*$, and this can be determined by performing a nonlinear stability analysis of that fixed point (De Leenheer et al. 2017; Appendix A). A resident migration propensity ϕ^* is a CSS whenever the horizontal line through, but excluding the point (ϕ^*, ϕ^*) , lies within a positive region where the fitness function W is positive.

2.2.4 Sensitivities of ESS values

Once we calculated equations for ϕ^* under each form of density-dependent competition, we looked at how the value of ϕ^* responded to changes in s_i , a_i , and b_i , using arbitrary parameter values. Migrant parameter values were: $s_M = 0.6$, $a_M = 3.3$, $b_M = 0.0002$, and $\hat{x}_M = 4900$. Non-migrant parameter values were: $s_N = 0.4$, $a_N = 4$, $b_N = 0.0002$, and $\tilde{x}_N = 3000$. To look at the effect of a_i , we

varied it between 0.0001 and 10, for the effect of b_i we varied it between $1 * 10^{-6}$ and 0.002, for the effect of s_i we varied it between $1 * 10^{-6}$ and 1.

2.3 Results

Of the four different forms of density-dependent competition, within phenotype was the only form for which partial migration was an ESS and a CSS in all conditions (Figure 2.3). The between phenotype form never allowed for partial migration as an ESS or CSS, whereas the prior residence and migrant advantage did under some conditions. Specific results for each of the four forms of density dependence are as follows.

1. Within phenotype: $z_M = x_M$ and $z_N = x_N$.

In this case, (2.11) – (2.12) simplifies to

$$x_M^*(\phi) = \hat{x}_M \text{ and } x_N^*(\phi) = \tilde{x}_N,$$

and since (2.8) must hold, it follows that there is a unique solution $\phi = \phi^*$ to these equations, where ϕ^* is defined as:

$$\phi^* = \frac{\frac{s_N}{s_M}}{\frac{\tilde{x}_N}{\hat{x}_M} + \frac{s_N}{s_M}}. \quad (2.13)$$

Thus, in this case ϕ^* is the only candidate ESS, and the nonlinear stability analysis in Appendix A shows that it is a genuine ESS. The sign of $W(\phi, \phi')$

is summarized in Figure 2.3, and indicates that ϕ^* is also a CSS.

2. Between phenotype: $z_M = x_M + x_N$ and $z_N = x_M + x_N$.

In this case, (2.11) – (2.12) simplifies to

$$x_M^*(\phi) + x_N^*(\phi) = \hat{x}_M \text{ and } x_M^*(\phi) + x_N^*(\phi) = \tilde{x}_N,$$

and if we make the mild and reasonable assumption that $\hat{x}_M \neq \tilde{x}_N$, there are no solutions to these equations. Thus, there are no candidate ESS values, and the sign of $W(\phi, \phi')$ depends only on which of the 2 abundances is bigger, \hat{x}_M or \tilde{x}_N , see Figure 2.3. If $\hat{x}_M > \tilde{x}_N$, then $\phi^* = 1$ is the unique ESS/CSS. Similarly, if $\hat{x}_M < \tilde{x}_N$, then $\phi^* = 0$ is the unique ESS/CSS. This result expresses that when between phenotype density dependence occurs, the phenotype that would perform best in isolation (i.e., achieves the highest equilibrium abundance in isolation), will outperform the other phenotype when both compete in the same environment.

3. Prior residence: $z_M = x_M + x_N$ and $z_N = x_N$.

In this case, (2.11) – (2.12) simplifies to

$$x_M^*(\phi) + x_N^*(\phi) = \hat{x}_M \text{ and } x_N^*(\phi) = \tilde{x}_N.$$

For these equations to have a positive solution $(x_M^*(\phi), x_N^*(\phi))$, there must hold that $\hat{x}_M > \tilde{x}_N$, and then we can use (2.8), to show that there is a unique

solution $\phi = \phi^*$ with ϕ^* defined as

$$\phi^* = \frac{\frac{s_N}{s_M}}{\frac{s_N}{s_M} + \frac{\tilde{x}_N}{\hat{x}_M - \tilde{x}_N}}. \quad (2.14)$$

Thus, ϕ^* is the unique candidate ESS in this case, and the nonlinear stability analysis in Appendix A shows that ϕ^* is a genuine ESS. The PIP in Figure 2.3 also indicates that ϕ^* is a CSS.

On the other hand, if $\hat{x}_M < \tilde{x}_N$, there are no solutions to the equations above, and thus no candidate ESSs. In this case, $\phi^* = 0$ is the unique ESS/CSS.

4. Migrant advantage: $z_M = x_M$ and $z_N = x_M + x_N$.

The analysis of this scenario is analogous to that of prior residence, but reverses the role of migrants and non-migrants: If $\tilde{x}_N > \hat{x}_M$, there is a unique ESS/CSS $\phi = \phi^*$, with

$$\phi^* = \frac{\frac{s_N}{s_M}}{\frac{s_N}{s_M} + \frac{\tilde{x}_N - \hat{x}_M}{\hat{x}_M}}. \quad (2.15)$$

If on the other hand, $\tilde{x}_N < \hat{x}_M$, then $\phi^* = 1$ is the unique ESS/CSS. These possibilities are summarized in the PIP in Figure 2.3.

We identified species that experience each of the different forms of density-dependent competition (Figure 2.4). The response of ϕ^* to changes in s_i , a_i , and b_i were variable among the different forms of competition (Figure 2.5-2.7). The response of the within phenotype ϕ^* to all three parameters was non-linear.

The rate of change was greatest at low parameter values, but then declined as the parameter values increased. This indicates feedbacks for all three parameters. The between phenotype ϕ^* response was discontinuous and highlighted a threshold parameter value controlled whether the population was all migrant or non-migrant. The prior residence ϕ^* response was also discontinuous because of the \hat{x}_M and \tilde{x}_N conditions. For each parameter value there was a threshold in which the ϕ^* was all non-migrant or partially migratory. Note, the ϕ^* would never be equal to 1 (i.e., the population could never be all migrant) under any parameter values. There were values of a_i and s_i for which migrants or non-migrants could no longer sustain themselves in isolation. This is a condition required for our analyses (equation 2.7) and therefore we could not predict what would happen to the ϕ^* for those parameter values. ϕ^* was most sensitive to changes in a_N , s_N and b_M . The migrant advantage ϕ^* response was complimentary to the prior residence response. The conditions of \hat{x}_M and \tilde{x}_N led to discontinuous functions and for each parameter value there was a threshold in which the ϕ^* was all migrant or partially migratory. ϕ^* would never be equal to 0 (i.e., the population could never be all non-migrant) under any parameter values. However, there were values of a_i and s_i for which migrants or non-migrants could no longer sustain themselves in isolation. This is a condition required for our analyses (equation 2.7) and therefore we could not predict what would happen to the ϕ^* for those parameter values. ϕ^* was most sensitive to changes in a_M , s_M and b_N .

2.4 Discussion

There were three circumstances in which partial migration was an ESS and a CSS: the within phenotype form in all conditions, the prior residence form when $\hat{x}_M > \tilde{x}_N$, and the migrant advantage form when $\hat{x}_M < \tilde{x}_N$. These three circumstances have two characteristics in common. There was some value of ϕ in which migrant and non-migrant fitnesses were equal and the relative fitnesses had opposite responses to ϕ (i.e., one fitness increased while the other decreased).

There were also three circumstances in which a single phenotype was the ESS and the CSS: the between phenotype form in all conditions, the prior residence form when $\hat{x}_M < \tilde{x}_N$, and the migrant advantage form when $\hat{x}_M > \tilde{x}_N$. These three circumstances have two opposite characteristics to those when partial migration occurs. There was never a value of ϕ in which migrant and non-migrant fitnesses were equal and the relative fitnesses had responded to ϕ in the same direction (i.e., the fitnesses both increased or decreased).

These characteristics are helpful for identifying other forms of density-dependent competition and the circumstances that may (or may not) lead to balancing selection and partial migration. We analyzed four forms of density-dependent competition, but there are many others and they may occur at other life stages.

We were surprised that the only form that allowed for partial migration as an ESS/CSS under all arrangements of \hat{x}_M and \tilde{x}_N was the between phenotype form. Under this form of competition, phenotypes do not compete directly for a shared resource during reproduction, but competition in each is indirectly affected by the

propensity for migration. If, for example, migration propensity is high, competition among migrants will be high and, simultaneously, competition among non-migrants will be low. This result has been demonstrated previously (De Leenheer et al. 2017), and has been shown to be a mechanism for equal fitness, or frequency-dependent fitness (Taylor and Norris 2007). It is notable that this is true under even extreme conditions, such as when migrants have a much better combination of survival and fertility (i.e., $\hat{x}_M \gg \tilde{x}_N$). In such a circumstance, it seems reasonable to ask: why allocate offspring to a phenotype that does so much worse than the other? The answer is because there will always be some small density in which non-migrants can achieve fitness equal to the migrants (or vice versa).

Prior residence is sufficient for partial migration as an ESS/CSS when $\hat{x}_M > \tilde{x}_N$, but only non-migration is an ESS/CSS when $\hat{x}_M < \tilde{x}_N$. Conversely, migrant advantage is sufficient for partial migration as an ESS/CSS when $\hat{x}_M < \tilde{x}_N$, but only migration is an ESS/CSS when $\hat{x}_M > \tilde{x}_N$. The prior residence form has been well studied, particularly in the bird literature, and has been clearly demonstrated as a potential mechanism for partial migration (Kokko 2007, 2011; Kokko and Lundberg 2001). Our results are notable because partial migration is not simply a continuum between complete migration and no migration, as other authors have suggested (Chapman et al. 2011; Griswold et al. 2010; Taylor and Norris 2007). Instead, complete migration is never expected to evolve under this form of competition. Using a different model and method, Kokko and Lundberg (2001) found a slightly different result in that migration could be evolutionarily stable if non-migration produced a sink population. Assessing the circumstance of a sink

population (i.e., $\tilde{x}_N < 0$) did not meet our initial conditions, so we cannot directly compare to this result, however it indicates that there may be some additional cases where complete migration could evolve. Populations experiencing migrant advantage competition could be all migrant or partially migratory, but compete non-migration is never expected to evolve. There are no other models to compare with, but given the parallels with prior residence, it is possible that complete non-migration could occur if migration was a sink ($\hat{x}_M < 0$).

The between phenotype form is the only form that was not sufficient for partial migration under any conditions. Instead, the population was expected to be all migrant or all non-migrant, depending on the relative values of \hat{x}_M and \tilde{x}_N . Other studies have noted that it alone cannot lead to equal fitnesses (Griswold et al. 2011; Taylor and Norris 2007), but here we show that there are no cases for which partial migration is an ESS or CSS. The reason for this is because between phenotype competition does not lead to the negative frequency dependent fitness required for balancing selection (equal fitnesses). The fitness of each phenotype depends on the frequency of phenotypes, through its effect on the density, but the changes in frequency have identical effects on the fitnesses. Therefore, the fitnesses of both phenotypes increase or decrease together, they do not follow an opposite pattern. Another way to express this is that between phenotype competition creates a one dimensional feedback environment, whereas frequency dependence requires a two (or more) dimensional feedback environment (Heino et al. 1998).

The between phenotype result does provide some insight into how some populations may transition from completely non-migratory to completely migratory.

Under this form of competition, a population simply has a threshold and whichever phenotype has the higher fitness will dominate. If threshold conditions change, the population would go through a period of transition during which migrant and non-migrant individuals were present, but this coexistence would not be a stable state and the population would eventually become only one phenotype or the other. This threshold result, based on \hat{x}_M and \tilde{x}_N , could be a useful way to describe a process that ecologically could be quite complicated (Levey and Stiles 1992; Rappole and Jones 2003).

The sensitivities of ϕ^* to changes in s_i , a_i , and b_i were variable among the different forms of competition, but all were non-linear. Because the responses are non-linear, how a population responds will depend on its survival, gamete production, and degree of competition values. For example, if a population experiencing within phenotype competition has low migrant survival, an increase in migration survival will rapidly increase the ESS migration propensity (Figure 2.5). If the population has high migrant survival, an increase in migration survival may have little effect on the ESS migration propensity. This non-linear responses of migration propensity to survival (as well as gamete production, and degree of competition) are due to feed backs. As survival improves, competition during reproduction increases and fertility declines. This feedback has really important implications for management and conservation decisions. Improving survival seems like an obvious choice as a conservation goal, however, if the ultimate goal is to produce more migrants (as might be the case in a commercially important species, such as steelhead), improving survival might not produce as many migrants as desired.

The change in survival may need to be coupled with a decrease in competition to achieve the desired result.

Populations with the prior residence form would be more sensitive to changes in non-migrant survival and number of gametes than comparable changes to migrant survival and number of gametes (Figure 2.5-2.6). They would also be more sensitive to changes in migrant competition than non-migrant competition (Figure 2.7). They are more sensitive in the sense that changes in those parameter values have a greater effect on ϕ^* , but they also can lead to ϕ^* values over the full range of zero to one. The parameters to which they are less sensitive have a more limited effect on ϕ^* . For example, changes to a_N in a population with the prior residence form would change its ϕ^* from 0.9999 to 0. Changes to a_M in that same population would change its ϕ^* from 0 to 0.8 only. The differences in sensitivities are important information for conservation and management goals.

2.5 Conclusion

The four forms of density-dependent competition studied here cover a broad range of reproductive dynamics and can provide a basis for generating predictions in a wide range of taxa. Density-dependent competition during reproduction leads to balancing selection and allows for partial migration when two conditions are met. First, migrant and non-migrant fitnesses are equal at some migration propensity and second, the relative fitnesses have an opposite responses to ϕ (i.e., one increases while the other decreases). If these conditions are not met, balancing selection can-

not occur, and instead a single phenotype will be the ESS and the CSS. Data on competition between migratory and non-migratory phenotypes during reproduction, and at other life stages, is sparse. Given the important role of competition in the evolution and maintenance of partial migration, gathering empirical data on competition would provide valuable insights into how natural selection maintains multiple phenotypes, such as partial migration, and would improve predictions of how taxa may adapt to ongoing ecological changes.

2.6 Figures

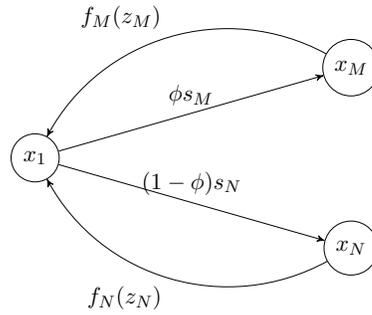


Figure 2.1: Population life cycle diagram for our general model of a partially migratory species. Juveniles (J) become migrant with probability ϕ or non-migrant with probability $(1 - \phi)$. Individuals that become migrant survive to adulthood with probability s_M and those that become non-migrants survive to adulthood with probability s_N . The number of juveniles produced is determined by a density-dependent fertility function ($f_i(z_i)$) that characterizes competition during reproduction. All individuals are semelparous.

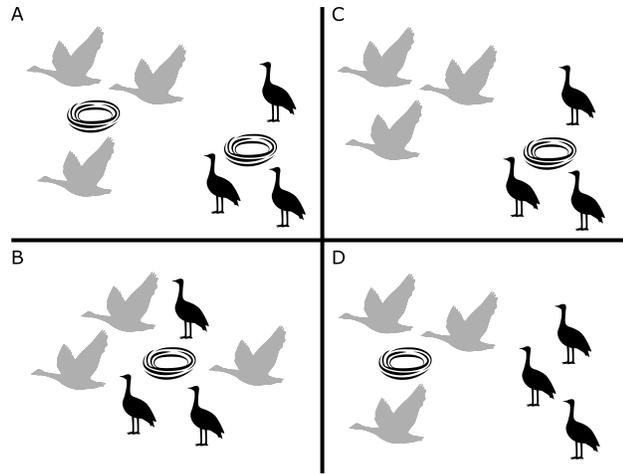


Figure 2.2: The four forms of density-dependent competition are illustrated here. Black standing geese represent non-migrants, the grey flying geese represent migrants, and the nest represents a resource individuals compete for, such as nesting habitats or mates. Within phenotype competition, in quadrant A, occurs when migrants and non-migrants compete only within their phenotype for a resource. Between phenotype competition, in quadrant B, occurs when migrants and non-migrants compete for the same resource. Prior residence, in quadrant C, occurs when non-migrants have the competitive advantage to migrants. This can occur through the prior residence effect (Kokko et al. 2006) or through superior competitive ability. Migrant advantage, in quadrant D, occurs when migrants have the competitive advantage to non-migrants, which could occur because of arrival time or competitive ability.

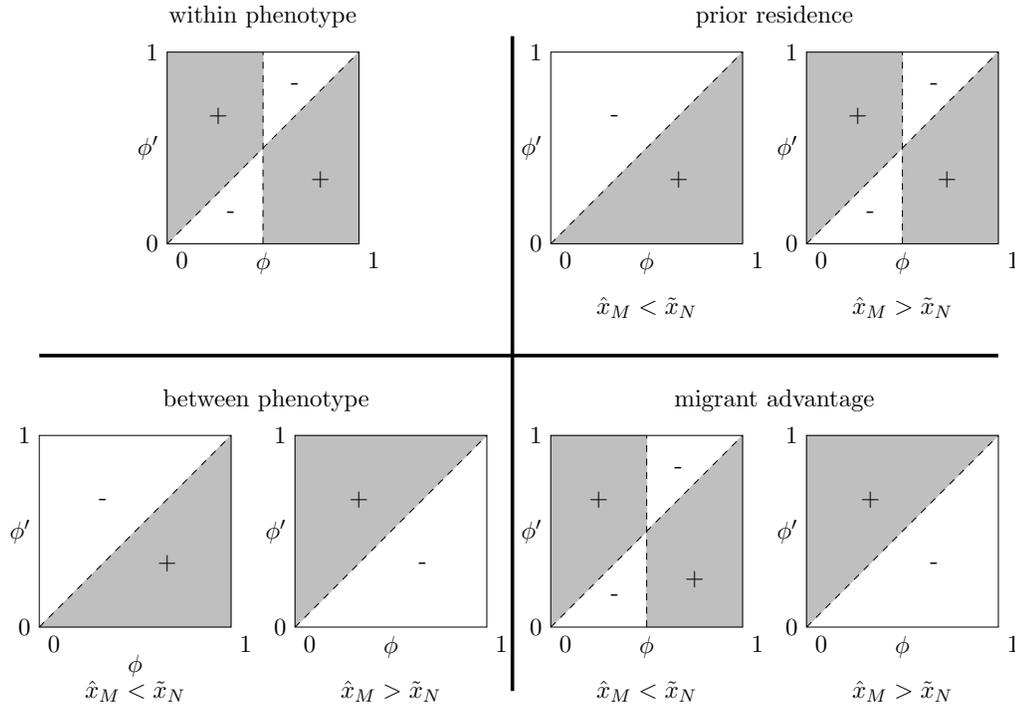


Figure 2.3: Pairwise invisibility plots (PIP) for each of the four forms of competition. In each PIP the resident migration propensity (ϕ) is on the x-axis and the mutant migration propensity (ϕ') is on the y-axis. The + sign, and grey coloring, indicates invasion by the mutant, while the - sign, and white coloring, indicates the mutant cannot invade the resident. In all but the within-phenotype form, the PIP depends on the conditions of \hat{x}_M and \tilde{x}_N , which are the number of migrant or non-migrant individuals in an all-migrant or all non-migrant population at population equilibrium, respectively (equation 2.7). The PIPs were generated from the mathematical proofs, not from specific parameter values.

| | |
|---|---|
| <p>Within Phenotype</p> <p>Female steelhead/ Rainbow trout (Zimmerman and Reeves 2000)</p> <p>Female Arctic charr (Jonsson and Hindar 1982)</p> <p>Female American dipper (Morrissey 2004)</p> | <p>Prior Residence</p> <p>Corys shearwaters (Perez et al. 2013)</p> <p>European Robin (Tobias 1997)</p> <p>European blackbird (Lundberg 1985)</p> <p>White-ruffed manakins (Boyle et al. 2008)</p> |
| <p>Between Phenotype</p> <p>Female red-spotted newts (Grayson and McLeod 2009)</p> <p>Female southern monarch (Slager and Malcom 2015)</p> | <p>Migrant Advantage</p> <p>Male Atlantic salmon (Weir et al. 2012)</p> |

Figure 2.4: Examples of species that experience different forms of density-dependent competition during reproduction. The list is not exhaustive and most of these examples were inferred based on descriptions of the mating system.

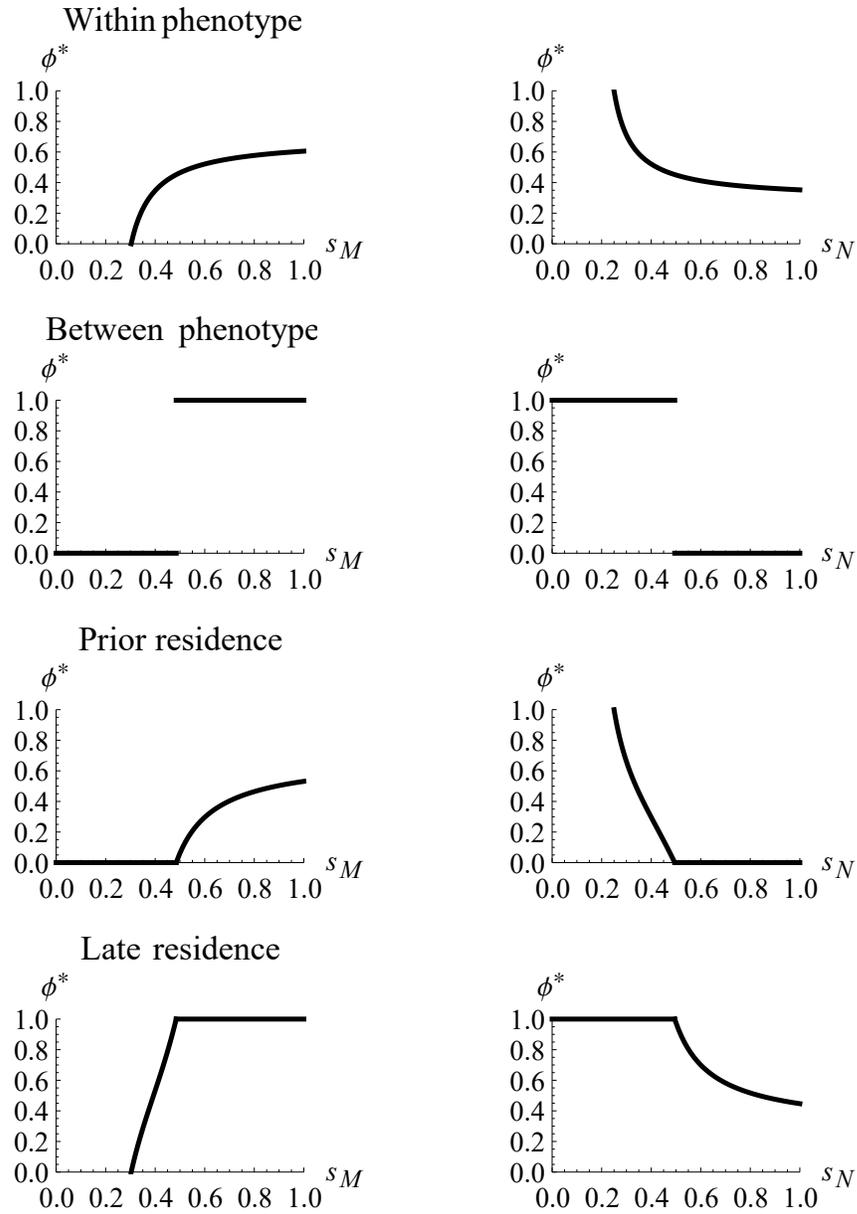


Figure 2.5: Responses of ϕ^* to changes in migrant and non-migrant survival values for each form of competition. Some ϕ^* values are not possible because survival is too low to sustain migrants or non-migrants in isolation (i.e., \hat{x}_M and \tilde{x}_N are less than zero).

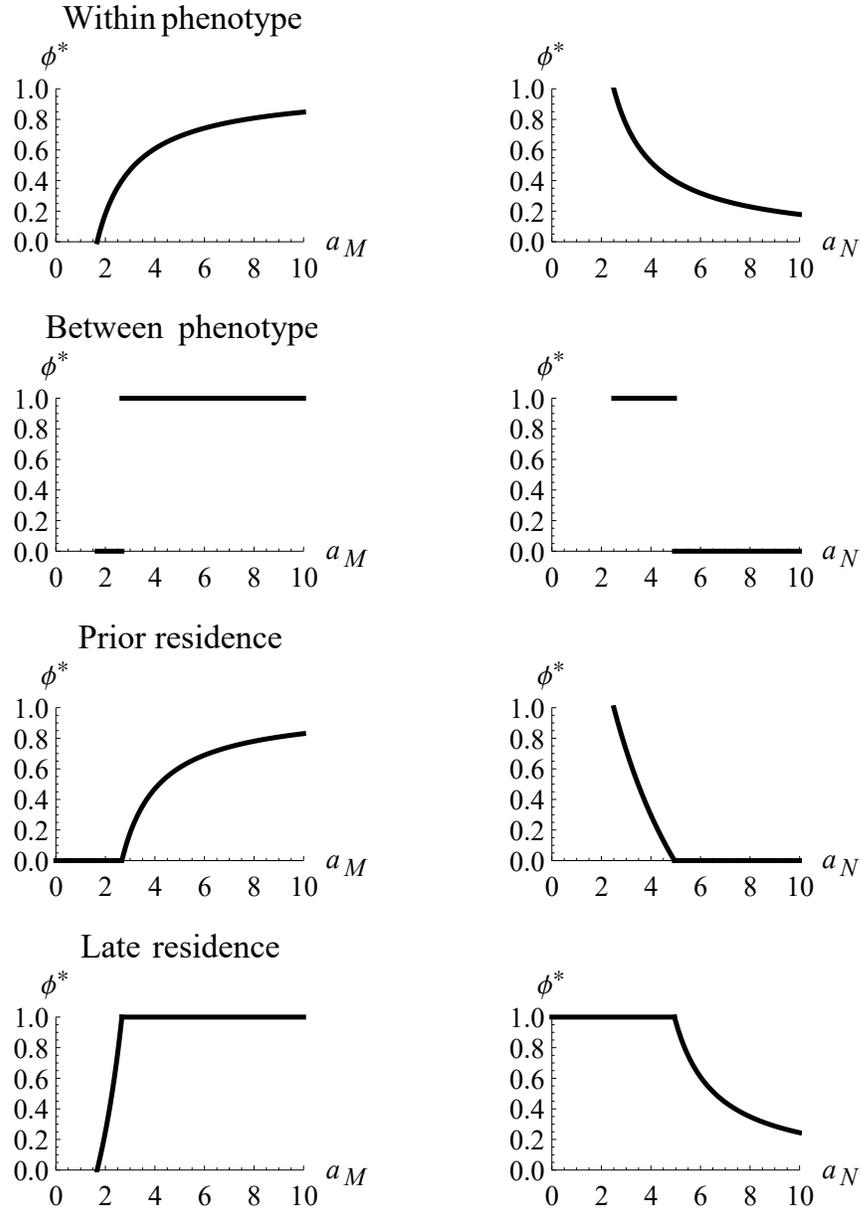


Figure 2.6: Responses of ϕ^* to changes in migrant and non-migrant gamete production (a_i) for each form of competition. Some ϕ^* values are not possible because the gamete production is too low to sustain migrants or non-migrants in isolation (i.e., \hat{x}_M and \tilde{x}_N are less than zero).

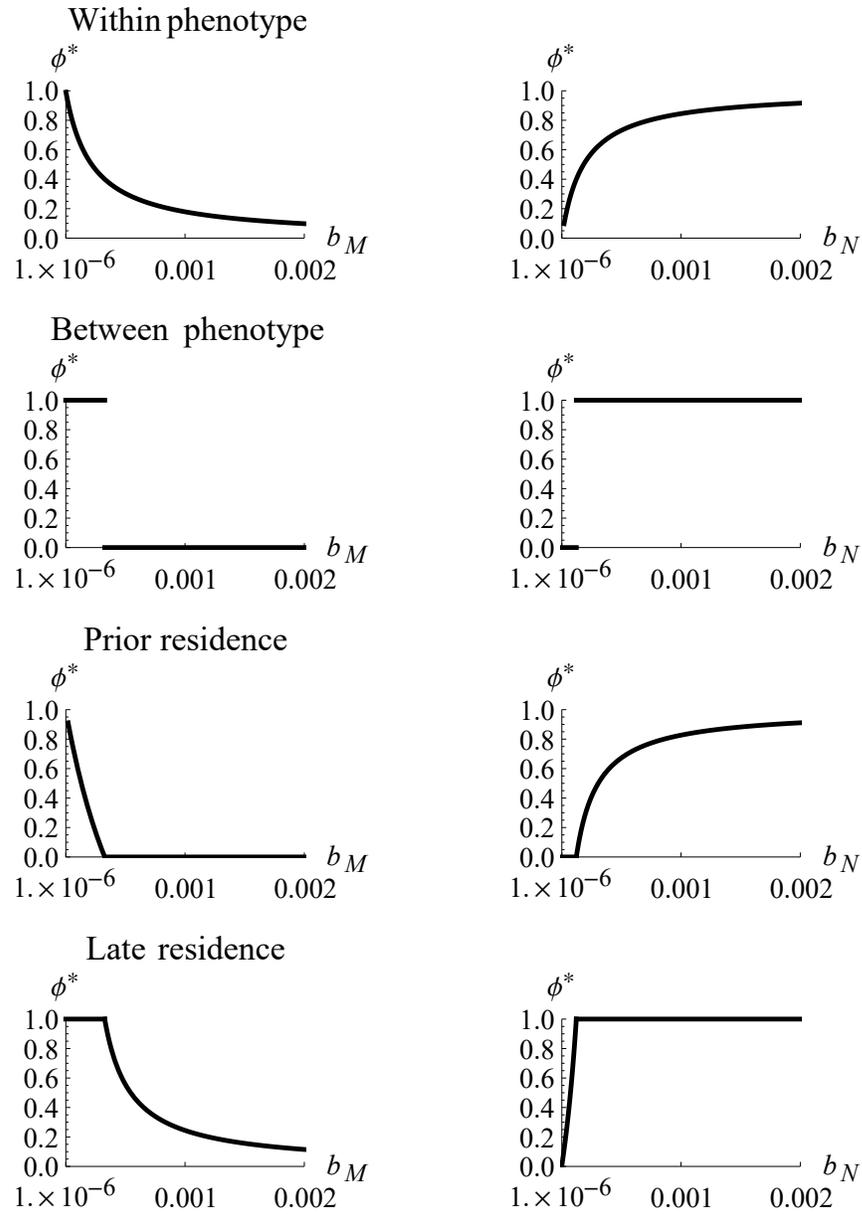


Figure 2.7: Responses of ϕ^* to changes in the migrant and non-migrant competition intensity (b_i) for each form of competition. As long as $b_i > 0$ there are no undefined ϕ^* values.

2.7 Table

Table 2.1: Partially Migratory Taxa

| Species | References |
|---|-------------------------------|
| <u>Birds</u> | |
| Cory's shearwater <i>Calonectris diomedea</i> | Perez et al. (2013) |
| House finch <i>Carpodacus mexicanus</i> | Able and Belthoff (1998) |
| American dipper <i>Cinclus mexicanus</i> | Morrissey (2004) |
| White-ruffed manakins <i>Corapipo altera</i> | Boyle (2008) |
| Yellow warbler <i>Dendroica petechia</i> | Klein and Brown (1994) |
| European robin <i>Erithacus rubecula</i> | Tobias (1997) |
| Dark-eyed junco <i>Junco hyemalis</i> | Rabenold and Rabenold (1985) |
| Great bustards <i>Otis tarda</i> | Alonso et al. (2000) |
| Blue tits <i>Parus caeruleus</i> | Smith and Nilsson (1987) |
| Willow tits <i>Poecile montanus</i> | Silverin et al. (1989) |
| Blackcaps <i>Sylvia atricapilla</i> | Pulido et al. (1996) |
| European blackbird <i>Turdus merula</i> | Lundberg (1985) |
| Tropical kingbird <i>Tyrannus melancholicus</i> | Jahn et al. (2010) |
| <u>Reptiles and Amphibians</u> | |
| Aldabra tortoise <i>Aldabrachelys gigantea</i> | Swingland and Lessells (1979) |
| Green turtles <i>Chelonia mydas</i> | Mortimer and Carr (1987) |
| Red-spotted newt <i>Notophthalmus viridescens</i> | Grayson and McLeod (2009) |
| <u>Mammals</u> | |
| Moose <i>Alces alces</i> | Ball et al. (2001) |
| Pronghorns <i>Antilocapra americana</i> | Feldhamer et al. (2007) |
| Roe deer <i>Capreolus capreolus</i> | Cagnacci et al. (2011) |
| Elk/Red deer <i>Cervus elaphus</i> | Mysterud et al. (2011) |
| Sika deer <i>Cervus nippon</i> | Sakuragi et al. (2003) |
| Wildebeest <i>Conochaetes taurinus</i> | Fryxell et al. (1988) |
| Daubenton's bat <i>Myotis daubentonii</i> | Senior et al. (2005) |
| Mule deer <i>Odocoileus hemionus</i> | Nicholson et al. (1997) |
| White-tailed deer <i>Odocoileus virginianus</i> | Nelson and Mech (1991) |
| Tibetan antelope/Chiru <i>Pantholops hodgsoni</i> | Schaller (1998) |
| African buffalo <i>Syncerus caffer</i> | Naidoo et al. (2012) |

Table 2.3: Partially Migratory Taxa continued

| Species | References |
|--|---------------------------------|
| <u>Insects</u> | |
| Common green darners <i>Anax junius</i> | May (2013) |
| Southern monarch <i>Danaus erippus</i> | Slager and Malcolm (2015) |
| <u>Fishes</u> | |
| Common bream <i>Abramis brama</i> | Skov et al. (2011) |
| Black bream <i>Acanthopagrus butcheri</i> | Gillanders et al. (2015) |
| Shortnose sturgeon <i>Acipenser brevirostrum</i> | Dadswell (1979) |
| European eel <i>Anguilla anguilla</i> | Tsukamoto et al. (1998) |
| Atlantic herring <i>Clupea harengus</i> | Ruzzante et al. (2006) |
| Bear Lake sculpin <i>Cottus extensus</i> | Neverman and Wurtsbaugh (1994) |
| Pike <i>Esox lucius</i> | Engstedt et al. (2010) |
| Cod <i>Gadus morhua</i> | Cote et al. (2004) |
| Three-spined stickleback <i>Gasterosteus aculeatus</i> | Kitamura et al. (2006) |
| Humpback chub <i>Gila cypha</i> | Yackulic et al. (2014) |
| Orange roughy <i>Hoplostethus atlanticus</i> | Bell et al. (1992) |
| White perch <i>Morone americana</i> | Kerr et al. (2009) |
| Cutthroat trout <i>Oncorhynchus clarki clarki</i> | Trotter (1989) |
| Masu salmon <i>O. masu</i> | Morita et al. (2014) |
| Rainbow trout/Steelhead <i>O. mykiss</i> | Shapovalov and Taft (1954) |
| Sockeye salmon <i>O. nerka</i> | Quinn (2005) |
| Chinook salmon <i>O. tshawytscha</i> | Larsen et al. (2013) |
| Smelt <i>Osmerus eperlanus</i> | Jonsson and Jonsson (1993) |
| Plaice <i>Pluronectes platessa</i> | Dunn and Pawson (2002) |
| Zulega <i>Prochilodus argenteus</i> | Godinho and Kynard (2006) |
| Spotted sorubim <i>Pseudoplatystoma corruscans</i> | Godinho et al. (2007) |
| New Zealand smelt <i>Retropinna retropinna</i> | Northcote and Ward (1985) |
| Roach <i>Rutilus rutilus</i> | Skov et al. (2010) |
| Atlantic salmon <i>Salmo salar</i> | Hutchings and Myers (1985) |
| Brown trout <i>S. trutta</i> | Jonsson (1985) |
| Arctic charr <i>Salvelinus alpinus</i> | Jonsson and Jonsson (2001) |
| Bull trout <i>S. confluentus</i> | Nelson et al. (2002) |
| Brook trout <i>S. fontinalis</i> | Morinville and Rasmussen (2003) |
| White-spotted charr <i>S. leucomaenis</i> | Morita et al. (2009) |
| Spiny dogfish <i>Squalus acanthius</i> | McFarlane and King (2003) |

Chapter 3 Evidence for Frequency-Dependent Selection in Female Steelhead and Rainbow Trout

3.1 Introduction

Partial migration, the coexistence of migratory and resident phenotypes, is common among fishes, particularly the salmonids (Chapman et al. 2012; Table 2.1). For evolutionary biologists through, salmonid partial migration is a perplexing system. Natural selection is generally considered a process that selects the single fittest phenotype, yet partial migration has two phenotypes, and often one appears to have lower fitness. This is particularly true for female salmonids. Resident females are almost always smaller than migratory females and because fecundity is proportional to body size, residents produce fewer eggs than migrants (Fleming and Reynolds 2004; Jonsson and Jonsson 1993; Kendall et al. 2015; Thriault et al. 2007). In some cases this difference can be extreme, with residents having ten times fewer eggs than migrants (Quinn et al. 2011; Schill et al. 2010). Resident females are assumed to have lower fitness than migrants because of their lower fecundity (Dodson et al. 2013; Satterthwaite et al. 2010). Although residency is more common in males, female residency occurs at low frequencies in the vast majority of salmonid species (see Dodson et al. (2013) for references). Predicting how these partially migratory species may adapt to climate change, land use,

management, and conservation actions is a high research priority for scientists and fishery managers (Apgar et al. 2017; Benjamin et al. 2013; Hendry and Stearns 2004; Satterthwaite et al. 2009, 2010). But, before we can successfully predict how salmonids will adapt to these pressures, we must first understand how partial migration is maintained.

The two main hypotheses for how natural selection leads to and maintains partial migration are frequency-dependent selection and the conditional strategy. Frequency-dependent selection occurs when the fitness of each phenotype depends on its frequency (Gromko 1977). If the fitness of each phenotype is greatest when it is rare (i.e., at low frequency), balancing selection will lead to the mixture of phenotypes where their fitnesses are equal (Charnov 1993; Kaitala et al. 1993; Lundberg 1987). Although the name focuses on the frequency of phenotypes, frequency-dependent selection can arise through density-dependent competition (Heino et al. 1998; Kokko 2007, 2011). The conditional strategy hypothesis focuses on the role of individual variation and proposes that individuals adopt a phenotype based on which will maximize their fitness, given their condition (Gross 1996; Hazel et al. 1990). This is sometimes referred to as ‘making the best of a bad situation’ because individuals with low condition can achieve a higher fitness by adopting one phenotype over the other (Lundberg 1987). The threshold, also called the switch point, determines the condition for which an individual should adopt one phenotype or the other. The threshold is located where the theoretical fitness functions of both phenotypes intersect (i.e., where the fitnesses of both types are equal).

Of these two hypotheses, the conditional strategy has received the most attention because there is considerable empirical data showing that migratory tendency is influenced by individual condition (Olsson et al. 2006; Paez et al. 2011; Phillis et al. 2016; Skov et al. 2010; Sloat et al. 2014). The frequency-dependent selection hypothesis has received less attention since there is little empirical evidence that the average fitness of migratory and non-migratory phenotypes are equal (Chapman et al. 2011), although the lack of evidence may simply be that calculating fitness is a challenge and is very rarely done. Even without the empirical evidence, there are two reasons frequency-dependent selection may still be important. First, density-dependent competition is commonly observed (Berejikian et al. 2010; Dijkstra et al. 2009), and there is theoretical evidence that it can lead to frequency-dependent selection (Heino et al. 1998; Kokko 2007, 2011). Additionally, if there are occasions when the less fit phenotype is more fit than the other (i.e., which phenotype has the higher fitness depends on the circumstances) the conditional strategy cannot maintain partial migration alone (Repka and Gross 1995). Under these circumstances frequency-dependent selection is the most likely mechanism for maintaining partial migration (Repka and Gross 1995). Therefore, frequency-dependent selection may be occurring through density-dependent competition or may be playing an under-appreciated role in the conditional strategy. If either of these is true, it may change predicted responses to future conditions, and thus, the role of frequency- and density-dependence warrants further consideration.

One of the problems with considering frequency-dependent selection among female migrants and residents is that it is difficult to conceptualize. Migratory

females are bigger than resident females, so they use habitats with larger gravel and deeper water (Clutton-Brock 2007; McMillan et al. 2015; Zimmerman and Reeves 2000). This segregates the spawning habitats, and sometimes spawn timing, which means that they do not compete between each other for this shared resource (Dodson et al. 2013). Competition for a shared resource is assumed to be a critical component of frequency-dependent selection (Berejikian et al. 2010; Dodson et al. 2013; Satterthwaite et al. 2010). However, recent theoretical work (De Leenheer et al. 2017, Chapter 2 this dissertation) has shown that a shared resource is not required for frequency-dependent selection and that competition within a phenotype can be the mechanism by which natural selection maintains partial migration.

In this paper we apply the recent theoretical findings of De Leenheer et al. (2017) to females of the partially migratory salmonid *Oncorhynchus mykiss*, commonly known as steelhead and rainbow trout. Steelhead is the migratory (anadromous) form and rainbow trout is the resident (freshwater) form of the species. First, we illustrate how density-dependent competition for spawning habitat can lead to frequency-dependent selection using a population simulation model. This relationship leads to partial migration as an evolutionary stable strategy (ESS). We then use the ESS equation derived by De Leenheer et al. (2017) to predict how a population's migration propensity may respond to changes in survival and reproduction. De Leenheer et al. (2017) showed mathematically that competition within phenotypes will always result in a migration propensity value between zero and one as an evolutionarily stable strategy (ESS), as long as both phenotypes can

sustain themselves independently (the definition of migration propensity is defined below). An ESS refers to a migration propensity value that has higher fitness than any other migration propensity arising by genetic mutation and competing in the existing population (Diekmann (2004)). A migration propensity ESS between zero and one will result in a partially migratory population. I predict how the ESS will change under three example scenarios. The three scenarios are increased migratory survival from improved dam passage, decreased competition for spawning habitat among rainbow trout due to additional spawning habitat from culvert replacements, and increased rainbow trout fecundity due to increases in latitude and food resources. I predict that increased migratory survival will lead to a higher ESS migration propensity, decreased competition for rainbow trout spawning habitat will decrease the ESS migration propensity (i.e., shift the population to more rainbow trout), and increased rainbow trout size and fecundity will also decrease the ESS migration propensity.

3.2 Methods

3.2.1 Frequency-dependent selection

Recall that frequency-dependent selection is defined as a process of selection in which the fitness of each tactic depends on the frequencies of the tactics (Gromko 1977). To determine whether female *O. mykiss* experience frequency-dependent selection, my approach was to calculate individual fitnesses in populations with

different frequencies of steelhead and rainbow trout and determine whether fitness depends on the frequencies.

I assumed that each individual has some ‘migration propensity’, denoted by the greek letter ϕ . This is the individual trait under selection. It can be thought of as an individual probability in the same way that the threshold in the conditional strategy model results in an individual probability for migration (Hazel et al. 1990). The probability ranges from zero to one, zero meaning there is no propensity for migration and all juveniles become rainbow trout, one meaning there is 100% propensity for migration and all juveniles become steelhead, and a value between zero and one meaning each juvenile has some probability of becoming a steelhead or rainbow trout. Notice that even though the migration propensity is an individual trait, it has population-level consequences. Individuals with migration propensities that equal zero or one lead to populations that are all steelhead or all rainbow trout, respectively. Individuals with migration propensities that are between zero and one lead to populations with a mixture of steelhead and rainbow trout.

In this context, migration propensity is the heritable component of the life history strategy. Steelhead offspring do not inherit genes to strictly migrate, they inherit a migration propensity. Likewise for rainbow trout. A population will have a single average migration propensity (i.e., steelhead and rainbow trout as tactics within a single strategy (Gross 1996; Hazel et al. 1990)).

Individual fitness is defined as lifetime reproductive success, which is the expected number of female eggs produced by a single female over her lifetime, and is denoted by R_0 (Caswell 2000; Roff 1996). Steelhead and rainbow trout each have

their own R_0^i value, where $i = S$ or R for steelhead and rainbow trout, respectively. Lifetime reproductive success (R_0^i) is calculated as the product of survival to reproduction (s_i) and the number of offspring produced ($f_i(x_i)$; De Leenheer et al. (2017)). Steelhead and rainbow trout fitnesses are given by:

$$R_0^S = s_S f_S(x_S), \quad (3.1)$$

$$R_0^R = s_R f_R(x_R). \quad (3.2)$$

I assume that survival to reproduction (s_i) is a long-term average, so survival values for steelhead and rainbow trout are constant in this model. I assume that the number of surviving offspring ($f_i(x_i)$) depends on competition for spawning habitat within a tactic. Steelhead and rainbow trout females use different sized gravel and water depths for spawning (Clutton-Brock 2007; McMillan et al. 2015; Zimmerman and Reeves 2000), and as such, there is only intraspecific competition. Competition is modeled with a Beverton-Holt function:

$$f_i(z) = \frac{a_i}{1 + b_i x_i}, \quad (3.3)$$

where $i = S$ or R for steelhead and rainbow trout, respectively, a_i is fecundity (i.e., the number of eggs) in the absence of competition, and b_i is a measure of the intensity of competition and the rate of fertility decline, and x_i is the number of steelhead or rainbow trout adults competing for redd habitat (Figure 3.1).

Notice that because fertility depends on the number adults, fitness also depends on the number of adults. Therefore, to calculate the fitnesses in populations with

different propensities for migration, I need to know the number of adults in each of these populations. This is achieved with a stage-structured population matrix model (Figure 3.2).

The population is represented by a three stage Leslie matrix model

$$\begin{pmatrix} x_1(t+1) \\ x_S(t+1) \\ x_R(t+1) \end{pmatrix} = \begin{pmatrix} 0 & f_S(x_S) & f_R(x_R) \\ \phi s_S & 0 & 0 \\ (1-\phi)s_R & 0 & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_M(t) \\ x_N(t) \end{pmatrix}, \quad (3.4)$$

where $x_1(t)$, $x_S(t)$ and $x_R(t)$ represent the abundances of juveniles, steelhead adults, and rainbow trout adults, respectively, at time t . Steelhead and rainbow trout contribute to a common pool of juveniles ($x_1(t)$) and all juveniles have the same propensity to migrate (ϕ). This individual propensity to migrate results in a fraction equal to ϕ becoming steelhead and the complimentary fraction $(1-\phi)$ becoming rainbow trout. Juveniles that become steelhead survive to adulthood with a probability s_S , and juveniles that become rainbow trout survive to adulthood with a probability s_R . Steelhead and rainbow reproduction is given by the tactic-specific density-dependent fertility function (equation 3.3).

This matrix model (equation 3.4) allows me to project the population size at any given time. The population will always reach an asymptotic size, known as population equilibrium, because of the density dependence in the model. To calculate and compare the fitnesses of populations with different migration propensities, I need to project the number of steelhead and rainbow trout at population equilibrium in populations with different values of migration propensity (ϕ). I do this

by using parameter values from (Table 3.1).

I used values of steelhead survival to reproduction that were ten times lower than rainbow survival to reproduction because I assume ocean migration causes higher mortality. I used values of fecundity that were 30 times greater for steelhead because of their larger body size. These values are generally based on values found in the literature (Quinn 2005). I used values of rainbow competition that were ten times lower than steelhead to represent a greater amount of spawning habitat for rainbow trout

I calculated the population equilibrium for populations with ϕ values ranging from zero to one, on intervals of 0.01, for a total of 101 populations. I defined population equilibrium as the population size when the dominant eigenvalue of the matrix (equation 3.4) equaled one for ten consecutive generations. The population size was the sum of juveniles, adult steelhead, and adult rainbow trout. The numbers of adult steelhead and rainbow trout were used to calculate the fertilities and fitnesses in 101 different populations, each with a different ϕ value.

3.2.2 Predictions based on evolutionarily stable strategy concept

We use the ESS equation derived by De Leenheer et al. (2017) to predict how a population's migration propensity may respond to three scenarios that change survival and reproduction. The ESS migration propensity is assigned the symbol

ϕ^* and is given by the equation:

$$\phi^* = \frac{\frac{s_R}{s_S}}{\frac{\tilde{x}_R}{\hat{x}_S} + \frac{s_R}{s_S}}, \quad (3.5)$$

where s_S and s_R are the survival to reproduction values for steelhead and rainbow trout, respectively, \hat{x}_S is the number of steelhead in a population with a migration propensity of one ($\phi = 1$; i.e., completely steelhead), and \tilde{x}_R is the number of rainbow trout in a population with $\phi = 0$ (i.e., all individuals are rainbow trout).

\hat{x}_S and \tilde{x}_R are given by the equations:

$$\hat{x}_S = \frac{a_S s_S - 1}{b_S} \quad (3.6)$$

$$\tilde{x}_R = \frac{a_R s_R - 1}{b_R}, \quad (3.7)$$

The ESS is globally stable and represents the migration propensity expected at the end point of natural selection. Notice that ϕ^* will always be a value between zero and one as long as both survival values, \hat{x}_S , and \tilde{x}_R are greater than zero. The ESS occurs at the migration propensity where the fitnesses of each tactic are equal (Figure 3.5).

I use equation 3.5 to predict how the ESS migration propensity (ϕ^*) will respond to increased migratory survival (s_S) from improved dam passage, decreased competition for spawning habitat among rainbow trout (b_R) due to additional spawning habitat from culvert replacements, and increased rainbow trout size and fecundity (a_R) due to increases in latitude and food resources. I used the param-

eter values in Table 3.1 as an example population and independently varied s_S , b_R , and a_R to assess its affect on ϕ^* . We varied s_S between 0 and 1, b_R between $1 * 10^{-6}$ and 0.4, and a_R between 0.1 and 4,000.

3.3 Results

The numbers of steelhead and rainbow trout in a population were determined by the migration propensity of the population. Populations with a high migration propensity had a greater number of steelhead, whereas populations with a low migration propensity had a greater number of rainbow trout (Figure 3.3). Because migration propensity affected the number of steelhead and rainbow trout, it affected their fertilities (Figure 3.1), and their fitnesses (Figure 3.5).

At low migration propensities, steelhead had relatively higher fitness, whereas at high migration propensities, rainbow trout had relatively higher fitness. The opposing directions of the relative fitnesses are evidence for frequency-dependent fitness and frequency-dependent selection. The intersection of the fitness curves is the expected value of migration propensity, or the evolutionarily stable strategy (ESS) migration propensity. It is notable that the migration propensity was not equal, or proportional, to the fraction of steelhead and rainbow adults, except when $\phi = 0$ or 1 (Figure 3.6).

The ESS migration propensity (ϕ^*) was more sensitive to changes in rainbow trout competition (b_R) than to changes in rainbow trout fecundity (a_R) or steelhead survival (s_S , Figure 3.7). Changes in fecundity and competition produced the full

spectrum of ϕ^* values, meaning ϕ^* ranged from approximately zero to one, although they never equal zero or one exactly. In contrast, ϕ^* reached an asymptotic value near 0.75 once survival increased above 0.002. The ESS migration propensity (ϕ^*) of the example population parameters equaled 0.76 and is denoted with a circle on the plots as a point of comparison. We found that the ESS migration propensity (ϕ^*) responded to survival and reproduction in the direction predicted, but all responses were non-linear, meaning the magnitude of response depended on the initial population. Our predictions were that increased migratory survival would lead to a higher ESS migration propensity (ϕ^*), decreased competition for rainbow trout spawning habitat would decrease the ESS migration propensity (i.e., shift the population to more rainbow trout), and increased rainbow trout size and fecundity would also decrease the ESS migration propensity.

3.4 Discussion

In this paper we sought to answer whether partial migration in female steelhead and rainbow trout could be maintained by frequency-dependent selection. The answer is yes, but frequency dependence arises in an unexpected way and requires some explanation. Frequency-dependent selection occurs when fitnesses vary as functions of the frequencies of tactics in the population and the rare tactic has the highest fitness (Gromko 1977). Implicit in this definition is that the number of individuals within each tactic cannot be independent. When the number of one goes up, the other must come down. One way to think of this is that there are

a fixed number of offspring that can be allocated to each tactic. For example, a clutch of 100 eggs could be allocated to steelhead or rainbow trout. Anytime more eggs are allocated to steelhead, fewer eggs must be allocated to rainbow trout. It is the same with migration propensity. Any time individuals have a higher migration propensity, fewer individuals will be rainbow trout. The fitnesses vary because of density-dependent competition for spawning habitat. Steelhead and rainbow trout fertilities decline as competition increases. The greater number of steelhead or rainbow in the habitat, the lower the per capita fertility. Steelhead and rainbow trout spawn in different habitats, so the number of steelhead do not directly affect rainbow trout fertility (or fitness), and vice versa. However, the fertility (and fitness) of each is indirectly affected by the number of the other, because a low migration propensity will mean a low number of steelhead but a high number of rainbow trout. A high migration propensity will mean a high number of steelhead and a low number of rainbow trout. As a result, the fitnesses do depend, albeit indirectly, on the frequency of steelhead (which is determined by the propensity of migration) and fitness is higher for the rare tactic (because of the density dependence). These two factors together lead to frequency-dependent selection. Similar results and conclusions appear in theoretical literature, but these are focused on the prior residence effect in partially migratory birds (Kaitala et al. 1993; Kokko 2007, 2011) and theoretical multidimensional environments (Heino et al. 1998).

That female *O. mykiss* should experience frequency-dependent selection is not obvious for two reasons. The first is that females do not compete for a shared

resource, so the density-dependent competition that affects the fertility of one phenotype does not directly affect the competition and fertility of the other (Clutton-Brock 2007; McMillan et al. 2015; Zimmerman and Reeves 2000). This is why negative frequency dependent selection is an often cited phenomenon in male *O. mykiss*, but not in females (Dodson et al. 2013; Satterthwaite et al. 2009). Second, the terminology itself is confusing. Does frequency refer to the juvenile or adult life stage and which is important for the selection? In female *O. mykiss*, and in other species that rely on a threshold trait (Roff 1996), the frequency at reproduction influences fitness, but the trait that determines the frequency, which is the trait under selection, is expressed at the juvenile stage. Therefore, even though fitness depends on the frequency of adult tactics, it is really the frequency during the juvenile stage that is important because it is the trait under selection.

This result highlights an important point about the term ‘frequency’ and the life stage at which selection occurs. Even though selection would favor the rare adult tactic during reproduction, it couldn’t act on the frequency of steelhead directly because it is not a trait. Selection must act on the trait responsible for the frequency of steelhead, which is the migration propensity.

An important observation was that the migration propensity and the frequency of adult steelhead are not equal unless $\phi = 0$ or 1 (Figure 3.6). The reason is because the numbers of adult steelhead and rainbow trout are affected by the migration propensity as well as the number of juveniles allocated by the migration propensity. This is important because the frequency of adult steelhead is what is most easily measured, yet it provides no information about the migration propen-

sity ESS value. If the goal is to measure the ESS, then it must be measured at the point of ‘decision’. The method of sex-ratio balancing that I describe in Chapter 4 is an example of a method that would estimate the ESS migration propensity.

That female *O. mykiss* experience frequency-dependent selection can be applied to predict how populations may adapt to altered environments. We considered the three scenarios of altered environments that included increased migratory survival from improved dam passage, decreased competition for spawning habitat among rainbow trout due to additional spawning habitat from culvert replacements, and increased rainbow trout size and fecundity due to increases in latitude and food resources. In all three scenarios our predicted direction of response matched the modeled direction of response, however the magnitude of change was unexpected (Figure 3.7). Changes to all three parameters (steelhead migratory survival, rainbow fecundity, rainbow competition intensity) resulted in non-linear responses of the ESS migration propensity (ϕ^*), meaning the magnitude of response depends on the initial population ESS value. One example is steelhead survival. If a population has survival and reproduction values such that its ESS migration propensity of 0.76 (indicated by the circle in Figure 3.7), increases in steelhead survival will have effectively no change on the ESS migration propensity. This is because of the feedbacks from the density-dependent competition and resulting frequency-dependent fitness. If steelhead survival increases, there will be more steelhead, but there will also be more steelhead competing for spawning habitat. This increased competition will decrease fertility and fitness. Therefore, a migration propensity does not improve fitness and would not be selected for.

These predicted responses have important implications for conservation and management. It is often assumed that increases in migration survival will lead to adaptations that make more steelhead (likewise, decreases in migration survival will lead to more rainbow trout). This may be true on the short-term, but our results indicate that long-term adaptations will not follow this pattern. An interesting consideration is how the survival and reproduction responses may act in combination. Changes that affect survival may also affect size or competition strength, and these interactions will have unique effects on the migration propensity ESS. This would be an interesting area of research, and we encourage a further look at this question.

Frequency-dependent fitness has not been included in previous *O. mykiss* models. Three studies have used a conditional strategy framework from Satterthwaite et al. (2009) to predict how *O. mykiss* will respond to changes in water temperature, food resources, and survival (Benjamin et al. 2013; Satterthwaite et al. 2010). Each found evidence that populations could become completely steelhead, or completely rainbow trout, depending on the growth and survival conditions. However, the framework does not include frequency- or density-dependencies, and our results indicate these dependencies can create important feedbacks that may change the outcomes. Adding density-dependent competition into the Satterthwaite et al. (2009) model would be an interesting study.

In conclusion, density-dependent competition and frequency-dependent selection likely play important roles in maintaining partial migration in female *O. mykiss*. The conditional strategy has taken center stage in the *O. mykiss* liter-

ature, but we have shown that frequency-dependent selection is a likely product of the density-dependent competition for spawning habitat. Frequency-dependent selection leads to feedbacks between survival, reproduction, and migration propensity that should be considered in future models.

3.5 Figures

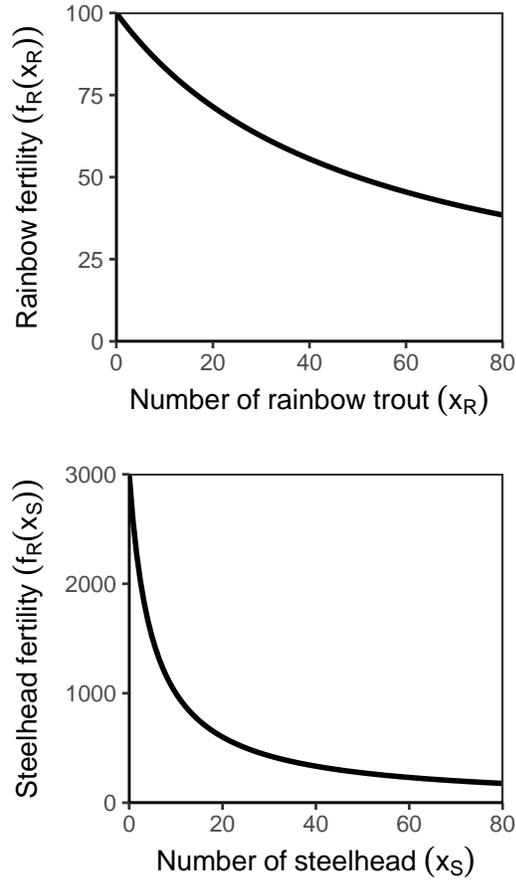


Figure 3.1: The per capita fertilities of steelhead and rainbow are Beverton-Holt functions that decline as the number of adult steelhead and rainbow competing for spawning habitat increases (equation 3.3). These plots were drawn using the parameters in Table 3.1. Steelhead and rainbow trout fertility in the absence of competition ($x_i = 0$) is equivalent to fecundity (a_i). The rate of decline is determined by the parameter b_i .

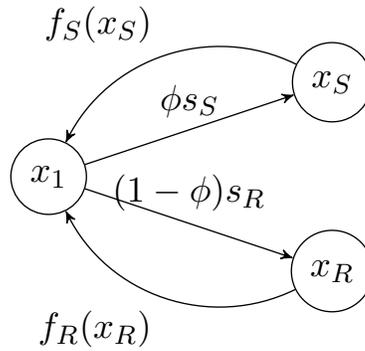


Figure 3.2: Population life cycle diagram for our general model of a partially migratory species. Juveniles (x_1) have a propensity for migration ϕ and become steelhead with a probability of ϕ or rainbow trout with a probability of $(1 - \phi)$. Juveniles that become steelhead survive to reproduction with probability s_M and those that become rainbow trout survive to reproduction with probability s_N . The number of juveniles produced by each tactic is determined by a density-dependent fertility function ($f_i(x_i)$), where $i = S$ or R for steelhead or rainbow trout, respectively. All individuals are semelparous in this model.

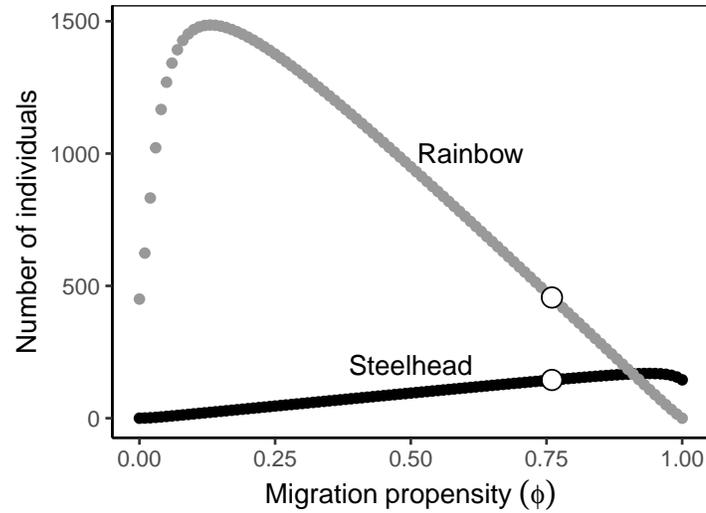


Figure 3.3: The number of adult steelhead and rainbow trout in populations that have migration propensities ranging from zero to one. As the population migration propensity approaches one, more juveniles become steelhead and the number of steelhead adults increases. Conversely, as the migration propensity approaches zero, more juveniles become rainbow and the number of rainbow adults increases. The highest number of steelhead and rainbow trout occurs at a migration propensity that greatly favors their tactic, but also produces some of the opposite tactic. Offspring of the opposite tactic boosts their numbers. The white circle at $\phi = 0.76$ is the evolutionary stable strategy (ϕ^*) of the example parameters. Notice that the ESS is not located at the highest population size.

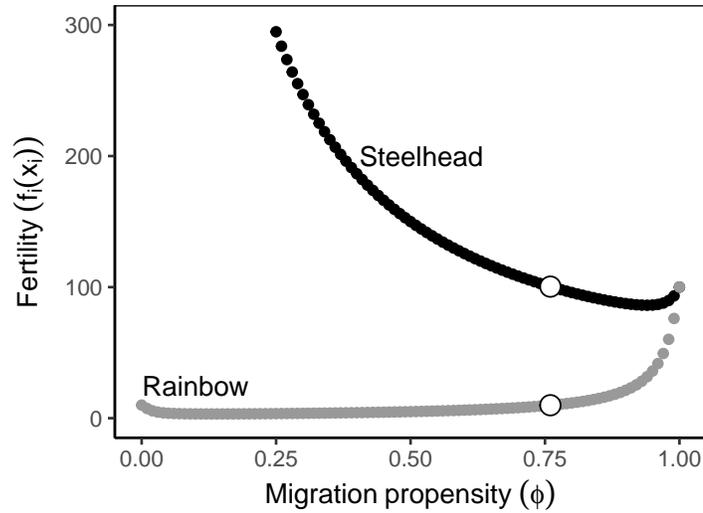


Figure 3.4: Steelhead and rainbow trout fertility ($f_i(x_i)$) as a function of migration propensity (ϕ). The y-axis is truncated at 300 so we can see the patterns at low fertilities. Steelhead fertility is highest when migration propensity is zero (which is not shown, steelhead fertility maxes out at 3000 when $\phi = 0$), whereas rainbow trout fertility is highest when migration propensity is one. The slight increase in steelhead fertility at $\phi = 1$ and rainbow trout fertility at $\phi = 0$ is surprising because this should be the point maximum density dependence. Instead, maximum density dependence occurs nearby because additional offspring are generated by the opposite tactic. For example, at $\phi = 0.98$ some juveniles become rainbow trout, whom produce juveniles that become steelhead. This is illustrated in Figure 3.3. The white circles at $\phi = 0.76$ mark the evolutionary stable strategy (ϕ^*) of the example parameters.

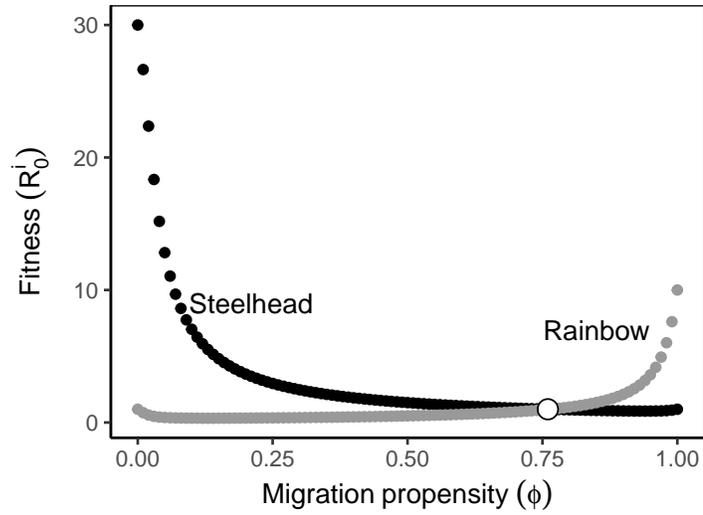


Figure 3.5: Steelhead and rainbow fitnesses (R_0^i) depend on the migration propensity of the population (ϕ). Fitness is highest for steelhead when the migration propensity is zero and fitness is highest for rainbow trout when the migration propensity is one. This is in-line with the commonly made statement that "fitness is highest for the rare tactic", except a more accurate description is that fitness is highest for the tactic with the lowest propensity of expression. The white circle is located at the ESS (ϕ^*) of the example parameters in Table 3.1.

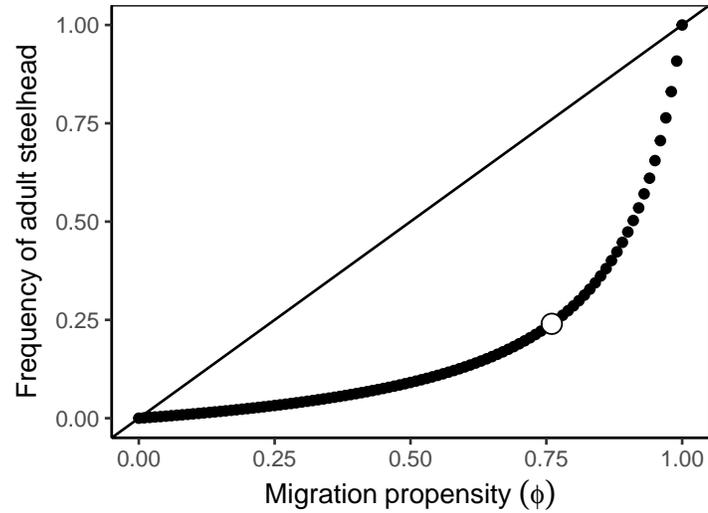


Figure 3.6: The frequency of steelhead (i.e., the proportion of steelhead adults in the population) is associated with the propensity for migration, but it is not a linear relationship. The diagonal line denotes where the frequency of steelhead equals the migration propensity. The frequency of steelhead is always lower than the propensity for migration because steelhead survival to reproduction is lower than rainbow trout survival to reproduction. The white circle is located at the ESS (ϕ^*) of the example parameters in Table 3.1. Note that at a migration propensity of 0.76, the frequency of adult steelhead in the population is only 0.24.

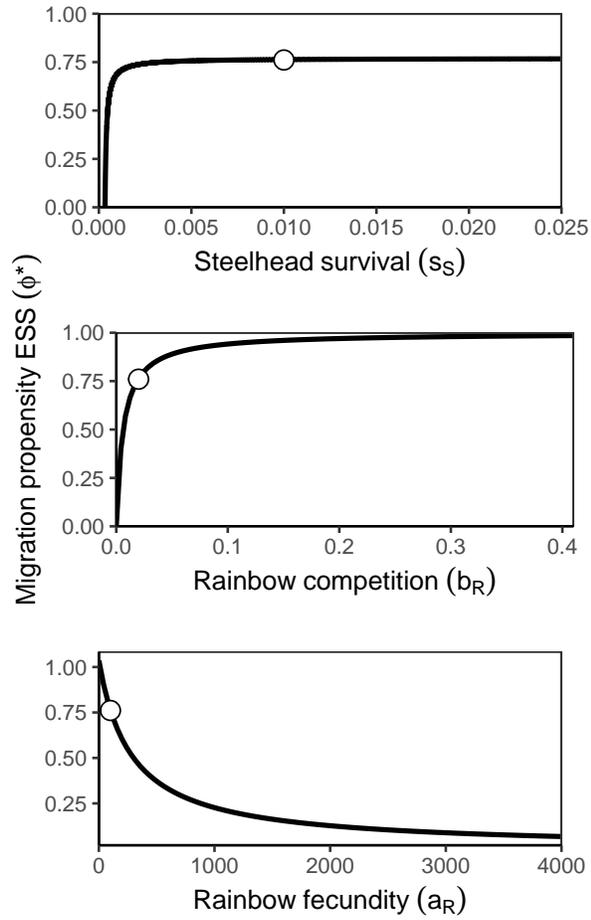


Figure 3.7: Survival (s_i), spawning competition (b_i), and fecundity (a_i) influence the migration propensity ESS (ϕ^*) in different ways. ϕ^* is more sensitive to changes in competition and fecundity in this example. The white circles are located at the ESS (ϕ^*) for the example parameters in Table 3.1.

3.6 Table

Table 3.1: Parameter values to illustrate steelhead and rainbow trout partial migration as an ESS

| | Steelhead | Rainbow |
|---------------------------------|-----------|---------|
| Survival (s_i) | 0.01 | 0.1 |
| Fecundity (a_i) | 3000 | 100 |
| Competition Intensity (b_i) | 0.2 | 0.02 |

Chapter 4 Estimating the Proportion of Migrants and Residents in Partially Migratory Species Using Sex-ratio balancing

Coauthors

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4.1 Introduction

Sex-biased movement patterns are common among migratory, partially migratory, and dispersing taxa (Dodson et al. 2013; Lawson Handley and Perrin 2007; McGuire and Boyle 2013). In these cases, one sex will migrate or disperse at a greater frequency than the other (e.g., Belthoff and Gauthreaux Jr 1991; Grayson and Wilbur 2009; Koizumi et al. 2006; Ohms et al. 2013), or the sexes will differentially select seasonal habitats (e.g., Kelly 1998; Ketterson and Nolan 1976; Kjelln 1994). Sex-specific migration and dispersal patterns lead to differences in survival (Johnson and Gaines 1990; Lucas et al. 1994), mating opportunities (Chapman et al. 2011), habitat use (Chapman et al. 2011), and selective pressures (Ronce 2007), which influence the genetics (Clobert et al. 2001; Wright 1969), mating systems (Lawson Handley and Perrin 2007), ecosystem dynamics (Chapman et al. 2011), and demographics (Clobert et al. 2001) of the population.

The effects of the sex-biased dispersal are additionally dependent on the overall proportion of migrants or dispersers in the population. For example, if the migrant sex ratio becomes more female biased, it is assumed that competition for migrant-specific breeding sites increases. However, if the overall proportion of migrants is low, a change in the migrant sex ratio may have a relatively small effect on migrant-specific competition for breeding sites. If the proportion of migrants is high, an increase in female migrants may lead to large changes in migrant-specific competition (Ohms et al. 2013). Despite this important interplay between the proportion of migrants/dispersers and sex-biased migration/dispersal, it is often ignored. The two main reasons for this are that the relationship between sex-biased movement and the proportion of migrants or dispersers has never been quantitatively defined, and empirical estimates of the proportion of migrants or dispersers in a population are difficult to collect and are thus rare.

In this paper, we address these issues by defining the relationship between sex-biased movement and the proportion of migrants or dispersers, and demonstrate how this relationship can be used as a method to estimate the proportion of migrants or dispersers. To our knowledge, there is no formally defined quantitative relationship between sex-biased movement and the proportion of migrants or dispersers. Our relationship and method are referred to as ‘sex-ratio balancing’. The general form of sex-ratio balancing makes it applicable to migration, partial migration, and dispersal, but for illustrative purposes we focus on partial migration. Partial migration is the phenomenon in which some individuals of a breeding population migrate seasonally to nonbreeding areas while others individuals of the same

population remain resident year-round (Chapman et al. 2011; Lack 1944). Partial migration is found throughout the animal kingdom and has been an important trait for understanding the evolutionary mechanisms that lead to coexistence of multiple life-history tactics (Cohen 1967; Kaitala et al. 1993; Lundberg 1987, 1988; Taylor and Norris 2007). Unfortunately, most of this work remains untested because of the methodological challenges associated with estimating the proportion of migrants.

Empirical estimates of the proportion of migrants require accurate counts of both migrants and residents, which are difficult to obtain. Organisms often migrate during seasons in which observation or capture is challenging, if not impossible (e.g., salmon migrate during seasonal floods; Quinn 2005), migrants and residents can be morphologically indistinguishable prior to migration, migration often takes place over large spatial scales, and sampling accuracy for migrants and residents can differ such that estimates are not comparable. Migration and partial migration research has employed a variety of tagging and tracking methods (Myserud et al. 2011; Perez et al. 2013; Rikardsen and Elliott 2000), which can be effective in some cases, but remain time consuming and expensive. Retrospective analyses (e.g., fish otolith analysis; Gillanders et al. 2015) or proxies of migration (e.g., the presence or absence of marine parasites on an adult fish; Kristoffersen et al. 1994) are also used, however these methods are system-specific and assessing their accuracy is difficult. These methodological challenges hinder research on the complex consequences of sex-biased migration and the evolutionary mechanisms that lead to partial migration and demonstrate the need for improved methods.

Here, we first lay out the conceptual framework for the relationship between sex-biased partial migration and the proportion of migrants, then define this relationship quantitatively. This relationship is referred to as sex-ratio balancing, and we demonstrate how it can be used to estimate the proportion of migrants using sex ratio measurements from the migrant and resident groups. We use a Bayesian approach to develop confidence bounds for the estimates, and extend the model by relaxing assumptions of age structure and equal mortality rates. Finally, the utility of sex-ratio balancing is demonstrated with examples from three different partially migratory taxa.

4.2 The Conceptual Model

Consider a population of partial migrants in which migrant and resident adults have offspring that become either migrant or resident. The sex ratio at birth is assumed to be 1:1 (male:female), and because we assume no sex-specific mortality at this stage, the sex ratio of juveniles is also 1:1. Some fraction of the juveniles become migrants and the remainder become residents. The fraction that becomes migrant is female biased and the fraction that becomes resident is male biased. We again assume there is no sex-specific mortality at the transition from juvenile to migrant or resident. Although there is now sex bias in the migrant and resident groups, the population-level sex ratio remains at 1:1. Because there is a limited number of males and females that can be assigned to each group, the sex bias in each group, and the relative proportion of the population assigned to each group,

are related.

This relationship is illustrated in Figure 4.1 using three scenarios. Each of the three scenarios begins with a 1:1 juvenile sex ratio. The proportion of the population assigned to the resident and migrant groups is different in each scenario, but the migrant sex ratio remains constant (i.e., 1:3). Because the relative proportion assigned to the resident and migrant groups changes in each scenario, the resident sex ratios are forced to change. It is this relationship between the sex ratios and proportion of migrants that leads to sex-ratio balancing as a method.

4.3 sex-ratio balancing

We define the following parameters:

ρ_g : Proportion migrant ($0 \leq \rho_g \leq 1$)

ρ_r : Proportion resident ($\rho_r = 1 - \rho_g$ and $0 \leq \rho_r \leq 1$)

π_g : Proportion of migrants that are female ($0 \leq \pi_g \leq 1$)

π_r : Proportion of residents that are female ($0 \leq \pi_r \leq 1$)

We assume the sex ratio is 1:1 at birth and, because there is no sex-specific mortality, remains 1:1 at the population level, even though females and males may adopt different migrant and resident tactics. This is equivalent to:

$$\pi_g \rho_g + \pi_r \rho_r = 0.5 \tag{4.1}$$

By substituting ρ_r with $(1 - \rho_g)$ equation (4.1) rearranges to:

$$\rho_g = \frac{0.5 - \pi_r}{\pi_g - \pi_r} \quad (4.2)$$

Equation (4.2) describes the proportion of migrants in a population as a function of the migrant and resident sex ratios. The importance of this relationship as a method lies with the sex ratios. Sex ratios are generally much easier to estimate than the proportion of migrants and require smaller sample sizes for a given level of confidence. Implicit is the simplifying assumption that individuals transition to a migrant or resident tactic at the same age. This simplification and the sex-specific mortality assumption are addressed in the Results section. One assumption that must not be violated is the sex-biased migration and residency assumption. Without a sex bias in either of the migrant or resident groups, the equation (4.2) goes to zero and cannot be used to calculate the proportion of migrants.

4.3.1 Error propagation and Bayesian highest posterior density intervals

To use sex-ratio balancing as a method it is important to understand how uncertainty in the sex ratio estimates (π_r and π_g) influences the proportion of migrant calculation (ρ_g). To do this, we calculate a 95% Bayesian highest posterior density (HPD) interval for ρ_g , which is interpreted as a 95% chance that the true value is contained in the HPD interval. We use a HPD interval rather than a posterior

interval to avoid any potential issues with asymmetric posteriors (Gelman et al. 2014). To calculate the HPD interval, we treat X_t as a binomial sample from a population of tactic t (either migrant (g) or resident (r)).

$$X_t \sim \text{Bin}(n_t, \pi_t) \quad (4.3)$$

Where n is the sample size, and π_t is the unknown proportion of females in tactic t . We assign bounded uniform priors for π_t .

$$\pi_g \sim \text{Uniform}(0.5, 1) = 2 \quad (4.4)$$

$$\pi_r \sim \text{Uniform}(0, 0.5) = 2 \quad (4.5)$$

These bounded priors reflect our assumption that migrants are female biased and residents are male biased, and to ensure that the posterior distribution is bound between 0 and 1. Female-biased migration is the most commonly observed bias among partially migratory species (Belthoff and Gauthreaux Jr 1991; Grayson and Wilbur 2009; Kjelln 1994; Senior et al. 2005; Dodson et al. 2013 and references therein; McGuire and Boyle 2013 and references therein; Ohms et al. 2013; Perez et al. 2013), and our priors reflect this. In dispersing taxa, both male- and female-biased dispersal is common (Lawson Handley and Perrin 2007). The priors can be adjusted to reflect a male-biased dispersal or migration pattern by assigning prior distributions of $\pi_g \sim \text{Uniform}(0, 0.5)$ and $\pi_r \sim \text{Uniform}(0.5, 1)$.

We calculate the posterior distribution of each π_t by using Bayes theorem and numerically integrating the denominator. We draw 10,000 random samples from

each posterior distribution and apply them to equation (4.2), such that,

$$\rho_g | \mathbf{X}_r, \mathbf{X}_g = \frac{0.5 - \pi_r^{(s)}}{\pi_g^{(s)} - \pi_r^{(s)}} \quad (4.6)$$

Where $s = 1, \dots, 10,000$ random draws. This generates a posterior distribution containing 10,000 values for ρ_g .

The 95% HPD interval for ρ_g is the set of values, C , satisfying,

$$\int_C f(\rho_g | \pi_g, \pi_r) d\rho_g = 0.95 \quad (4.7)$$

such that for any value of $\rho_g \in C$ and any value $\rho_g^* \notin C$, $f(\rho_g | \pi_g, \pi_r) \geq f(\rho_g^* | \pi_g, \pi_r)$.

4.4 Results

sex-ratio balancing defines the relationship between the proportion of migrants and residents and their sex ratios. As shown by the surface in Figure 4.2, some combinations of values cannot exist and would not be expected in nature. For example, a migrant sex ratio of 0.9 and a resident sex ratio of 0.4 cannot exist together with a high proportion of migrants in the population. Migrants and residents have complementary sex ratios (e.g., 0.8 and 0.2) only when the population is evenly divided between the two types (i.e., the proportion of migrants is 0.5). Any migrant sex ratio greater than 0.5 can be associated with a resident sex ratio between 0 and 0.5. Even if the migrants are exclusively female ($\pi_g = 1$), residents can have any sex ratio between 0 and 0.499. The Bayesian 95% HPD interval is interpreted as

the 95% chance the true value is contained in the interval and characterizes the uncertainty associated with the estimate of ρ_g . It is based on the sex ratio sample sizes and prior information about the migrant and resident sex ratios.

4.4.1 Allowing differential mortality

In equations (4.1) and (4.2), we assume that males and females experience equal mortality between birth and their ‘decision’ to migrate or not. To assess how this assumption influences the estimate of ρ_g , we replace the 0.5 with a sex-specific mortality term, such that:

$$\gamma: \text{proportion of females prior to transition, } (0 \leq \gamma \leq 1) \quad (4.8)$$

Substituting this into equation 4.2 yields:

$$\rho_g = \frac{\gamma - \pi_r}{\pi_g - \pi_r} \quad (4.9)$$

From equation (4.9), it is clear that sex-specific mortality directly influences ρ_g . However, if the sex-specific mortality is known, it can be directly added to the model through the parameter γ . Therefore, although sex-specific mortality is highly influential on ρ_g , it can also be easily added to equation (4.2) if necessary.

It is important to note that sex-specific mortality is influential only at life stages prior to the transition from juvenile to migrant or resident (i.e., prior to the time period before the sex ratios are measured). For example, if sex ratios are mea-

sured immediately after the transition from juvenile to migrant or resident, any sex-specific mortality that takes place later in life does not influence the sex-ratio balancing. A common example of this is differential mortality after reproduction, in which either males or females experience greater mortality from fighting, increased risk taking, or additional energy output (Adler and Bonduriansky 2011). Therefore, it is important to know the life history and the stage (or age) of the organisms at the time of sex ratio measurement.

4.4.2 Addition of age structure

We made the simplifying assumption that the transition from birth to migration or residency takes place at the same age, in equations (4.1) and (4.2). However, in many taxa this transition takes place over multiple years. For example in one study of the partially migratory salmonid *Oncorhynchus mykiss*, individuals became migrants or residents between one and five years of age (Ohms et al. 2013). To explore the consequences of relaxing this assumption, we create a two-age model in which a fraction individuals transition to migrant or resident in year one, and the remaining fraction transitions in year two (Figure 4.3). This framework could be expanded to include more ages, but for the purposes of demonstration we use only two ages.

Let,

ρ_{t1} : Proportion of tactic t at age 1

ρ_{t2} : Proportion of tactic t at age 2

π_{t1} : Proportion of females in tactic t at age 1

π_{t2} : Proportion of females in tactic t at age 2

η : Proportion that transition at age-2

where tactic (t) is either migrant (g) or resident (r).

We start with the assumption used previously in equation (4.2), in which the number of resident and migratory females equals the number resident and migratory males (i.e., half of the population). Expanding to two cohorts, equation (4.2) becomes:

$$\rho_{g1}\pi_{g1} + \rho_{r1}\pi_{r1} + \eta(\rho_{g2}\pi_{g2} + \rho_{r2}\pi_{r2}) = 0.5 \quad (4.10)$$

From equation (4.10) it is apparent that

$$\rho_g = \rho_{g1} + \eta\rho_{g2} \quad (4.11)$$

$$\pi_g = \phi_1\pi_{g1} + \phi_2\pi_{g2} \quad (4.12)$$

where ϕ_1 and ϕ_2 are the proportion of age-1 and age-2 migrants, respectively.

Notice that π_g is equivalent to the weighted average of the sex ratios in each age class. This indicates that if the resident or migrant sex ratios are measured

while ignoring the relative abundances of each age class, some ages could be over- or under-represented and the measured sex ratio would not accurately reflect that of the group. This error could lead to an inaccurate estimate of ρ_g , but the degree of inaccuracy depends on the amount of difference in the sex ratios of the different age groups. If the sex ratios among age groups are similar, there will be relatively small effect on ρ_g .

4.5 Applications in Three Taxa

We apply sex-ratio balancing to estimate the proportion of migrants (or residents) in three published data sets to demonstrate how sex-ratio balancing could be useful for current data and its applicability to many taxa and environments. None of these studies were designed with sex-ratio balancing in mind, and as such, the conclusions we draw should be treated with caution. The purpose of this section is to demonstrate applications in a variety of systems and to highlight the possibilities of this method.

4.5.1 Bats

The Daubenton's bat (*Myotis daubentonii*) is a small insectivorous species common throughout Europe. These bats congregate at high elevation upland caves to mate in the fall, and hibernate at these locations through winter. Once summer arrives the bats come out of hibernation. A fraction of the population then migrates to

lower elevation areas to feed, while others remain in the high elevation upland areas (Senior et al. 2005). Data from several closely related species suggests that upland residents tend to be male, likely because females have higher energetic requirements that necessitate migration to the more productive lowland areas (Barclay 1991).

Senior et al. (2005) monitored the sex ratios of migratory and resident *M. daubentonii* in the central UK for six years. By combining data for six years, they found a resident bat sex ratio of 126:1 (n=127) and a migrant sex ratio of 1:1.45 (n=108). All bats collected were between 1 and 8+ years old and there was no difference in the age frequency of individuals in the migratory and resident groups. In the absence of age-specific sex ratios, we assume no difference in sex ratios by age class. We also assume there was no sex-specific or tactic-specific mortality.

Using ratio balancing, we estimate that 83.9% of the bats in this population were migratory (95% posterior HPD interval 72.8 to 97.3%, Figure 4.4). Senior et al. (2005) did not estimate the proportion of migrants, but our HPD interval is consistent with the cases where the majority of residents were males (Figure 4.2).

Senior et al. (2005) concluded that the less competitive males were excluded from the high quality, lowland habitat during the summer and were forced to remain as residents in the high elevations. This suggests that the amount of low elevation habitat could influence the proportion of migrants in this bat population. Ratio balancing could be used to assess whether the amount of low elevation habitat is related to the proportion of migrants and provide insights into factors that control the demographics of this population.

4.5.2 Pelagic seabirds

The Cory's shearwater (*Calonectris diomedea*) is a pelagic seabird that breeds February to November on islands in the Canary current (Granadeiro 1991). Most individuals undertake winter migrations to one of five possible areas in the Southern Atlantic ocean, while the remaining individuals overwinter as residents near the breeding area (Dias et al. 2011).

Perez et al. (2013) followed migrant and resident Cory's shearwaters that bred on Selvagem Grande Island using geolocators and isotopes from 2006 to 2011. They found that the sex ratio of resident birds was 14:1 (n=15), and the sex ratio of migratory birds was 1.04:1 (n=157). These sex ratios were calculated from data combined over the 6 year study.

Age data were not reported in this paper, however the study found that migratory decision was not affected by year or the age of birds (using a generalized linear model with a logit link function). There was some evidence that adult birds could change between migratory and resident tactics, although the sample size was limited to only seven birds that were tracked for more than one year. Three of the seven birds changed from migratory to resident on at least one occasion; given this small sample size it is not clear whether this switching is representative of the population, so we ignored it for this analysis.

In the absence of data, we assume there was no difference in sex ratios by age class or sex- and tactic-specific mortality. Using the sex ratios reported, we estimate that 94.7 of the shearwater population was migratory (95 posterior HPD

interval 84.9 to 99.9, Figure 4.4). Perez et al. (2013) estimated that 91.9 of studied birds (n=172) were migratory using isotopes and geolocators. Their estimate falls within our 95 HPD interval and is only slightly less than our estimate, indicating concordance between these two disparate methods for estimating proportion of migrants.

This example demonstrates how ratio balancing can provide comparable estimates of the proportion of migrants with relatively simple observational data. Sex ratio data collection is much easier and cost-effective than geolocation or isotopes, and if it was the focus of the study, it could lead to increased sample size and better estimates of the proportion migrants.

4.5.3 Salmon

The Chinook Salmon (*Oncorhynchus tshawytscha*) is a culturally and economically valuable fish species native to the northern Pacific Ocean. Spawning takes place during summer or fall in freshwater streams. Migrants move to the ocean in the spring, and residents remain in freshwater to mature and later spawn. We use the terms resident and migrant to describe the general patterns of maturing in freshwater or migrating to the ocean, respectively. It is important to note that there can be considerable diversity in the ages and behaviors within these migrant and resident categories, both within and among populations. For example, some residents may migrate hundreds of kilometers within a river system (i.e., are adfluvial), while others remain near their natal spawning site (Larsen et al. 2013).

This complexity could be included in other sex-ratio balancing analyses, but in this example we limit the analysis to the general categories of migrant and resident.

Larsen et al. (2013) measured the sex ratios of wild and hatchery-bred migratory Chinook Salmon in the Yakima River of Washington State, USA for seven years. The high frequency of residents among hatchery Chinook has concerned biologists, but because of difficulties in sampling wild resident Chinook, it is unclear whether the high frequency of residents in hatchery-bred fish is abnormal compared to wild fish (Pearsons et al. 2009). In the Yakima River, migratory wild and hatchery-bred Chinook Salmon migrate to the ocean after approximately 17 months in freshwater. Residents remain in freshwater and spawn at age one or two (Larsen et al. 2013; Pearsons et al. 2009). Female residency is extremely rare (Harstad et al. 2014; Healey 1991), whereas male residency can be quite common, especially among hatchery-bred fish (Harstad et al. 2014; Larsen et al. 2013).

During the spring outmigration Larsen et al. (2013) measured the sex ratios in both wild and hatchery migrants at a dam 260 river kilometers downstream from the hatchery. Hatchery fish had been artificially spawned fish at a hatchery on the Yakima River and released after 17 months. Sex ratios ranged from 52% female to 68% female.

To calculate the proportion of residents using sex-ratio balancing we assumed that all females were migratory because no resident females were observed in the seven years of the Larsen et al. (2013) study, and, according to Harstad et al. (2014) and Healey (1991), resident females are extremely rare. We assigned the resident sex ratio a value of 1:0 male:female, which simplified equation (4.2) to $0.5/\pi_g$.

Additionally, we assumed that all migrants were 17 months of age, residents were either age one or two, and there was no age or sex-specific mortality prior to this transition. There was no sex-specific mortality among the hatchery-bred fish prior to release (Larsen et al. 2013); however this data was not collected in wild fish.

We calculated the proportion of residents and the 95% HPD intervals for both wild and hatchery groups in each of the seven years using sex-ratio balancing (Figure 4.5). We found no consistent differences between the calculated proportion of residents in wild and hatchery-bred fish (Figure 4.5). The median proportion of residents ranged from 0.268 to 0.046. The 95% HPD intervals overlapped in every year except for 2001, and there was no consistent pattern in which group had the higher proportion of residents (Figure 4.5). These results indicate that hatchery Chinook did not have a consistently higher proportion of residents in the Yakima River population from 2001 to 2007.

Few studies have directly compared the proportion of residents in wild and hatchery-bred Chinook (although, see Pearsons et al. 2009). The lack of a consistent pattern in our Chinook analysis could indicate that the differences between hatchery-bred and wild Chinook may be more population-specific than previously expected, at least at the broad categorization of migrant and resident. Within these categories there is evidence that the age of maturation differs (i.e., hatchery fish mature at age one only, whereas wild fish mature at age one or two, Pearsons et al. 2009) and this has important implications for the age and mortality assumptions used in our analysis, as well as the species management. Additional data on ages of freshwater residents and mortality should be incorporated into any

future sex-ratio balancing analysis through equations similar to those presented in equations (4.9) and (4.10).

4.6 Discussion

The proportion of migrants in a population is critical component for understanding the effects of sex-biased migration as well as the causes and consequences of partial migration. In this paper, we present the first formally defined quantitative relationship between migrant and resident sex ratios and the proportion of migrants. We demonstrate how this relationship can be leveraged as a method to estimate the proportion of migrants through sex-ratio balancing. sex-ratio balancing can be applied to a variety of organisms that inhabit a wide range of habitats, and has explicit, testable assumptions.

We present a basic version of sex-ratio balancing that assumes a 1:1 primary sex ratio, a single age transition from juvenile to migrant or resident, and no sex-specific mortality prior to the transition. Although these assumptions are adequate in some cases, they will not apply universally and will need to be adjusted to accommodate more complicated scenarios. We demonstrate how to incorporate deviations from the 1:1 starting sex ratio and additions to the age structure, but exactly how these are adjusted will depend on the study system and the research questions. We also limited the examples to broadly defined ‘migrant’ and ‘resident’ categories. These categories may not completely describe the life history diversity within a taxa (e.g., the Chinook example from Larsen et al. 2013) and additional

categories may be necessary to meet the specific needs of a study system.

A key benefit of sex-ratio balancing is that it requires sex ratio data from the migrants and residents, which can often be collected in a non-lethal manner and is much easier to quantify than the numbers of migrants and residents. Non-lethal sex determination methods vary by taxa and include visual inspection (i.e., Senior et al. 2005), morphological measurements or vocalization identification (i.e., Perez et al. 2013), ultrasound (i.e., Bonar et al. 1989), or genetic identification (i.e., Ohms et al. 2013). Non-lethal sex or life history determination is not possible for all taxa, however, and this consideration is especially important for endangered species act listed species whose sample availability may be considerably restricted.

The Bayesian HPD interval associated with sex-ratio balancing is unique among currently available methods and provides an estimate of the uncertainty associated with the proportion migrant estimate. None of the current methods for estimating the proportion of migrants (e.g., tagging and tracking, retrospective analysis, or proxies) provide measures of uncertainty, which limits comparisons between populations. The HPD interval in sex-ratio balancing is controlled by sample size, the proportion values, and prior information about the sex ratio values. If sex ratio values are known from previous studies, they can be incorporated directly and will decrease the HPD interval width. In our three examples, the priors reflected a general assumption that migrant sex ratios are female-biased and range from 0.5 to 1, but each of these could be more specific by incorporating prior information. The use of prior information could be particularly beneficial to long-term studies because as the priors become more specific the sample sizes needed for a given

degree of certainty decrease.

One possible extension of ratio balancing is in estimating population sizes. Once the proportion of migrants has been estimated through ratio balancing, it could be combined with an estimate of the number of migrants in a population to infer the number of residents (or vice versa). For example, the number of migrating juvenile salmon are often estimated at large traps as they migrate to the ocean. The estimated number of migrants could be combined with a proportion migrant estimate to infer the number of residents in that population. This extension requires additional assumptions and analysis, but it could be a very useful tool for estimating population sizes when one component of the population is difficult to sample.

Ratio balancing also has potential applications for sex-biased dispersal or specific migratory patterns, such as sex-biased latitudinal migration in birds (Belthoff and Gauthreaux Jr 1991). Estimating the proportion of dispersers remains an understudied component of dispersal due to methodological challenges similar to those in partially migratory systems. Meeting the necessary assumptions could be a challenge and may limit the applications within dispersal. For example, in dispersing species, dispersal may take place over many years and in multiple cohorts, and immigrants from other populations are morphologically identical and impossible to separate from the local population. Likewise, in sex-biased latitudinal migrations, there may be multiple breeding populations migrating to the same locations making it impossible to measure the sex ratios in each population. However, not all populations will be this complicated and some of this additional

variation could be incorporated into the sex-ratio balancing approach.

In conclusion, sex-ratio balancing is a unique method for estimating the proportion of migrants that could be useful for a variety of taxa. It also provides a much needed quantitative link between sex biased movement and the overall proportion of migrants in a population. Both the method and quantitative relationship are directly beneficial to management and conservation actions, such as setting restoration goals, prioritizing habitat conservation or movement corridors, predicting susceptibility to climate change, and assessing harvest consequences (Brenkman and Corbett 2005; McGuire and Boyle 2013; Moore et al. 2014), ultimately leading to better-informed conservation and management decisions and a better understanding of partially migratory species in general.

4.7 Figures

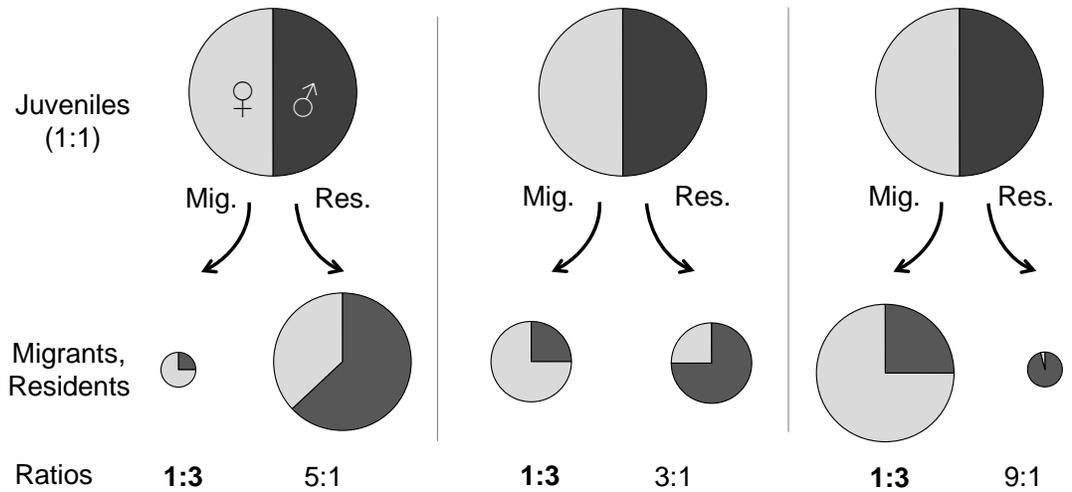


Figure 4.1: An illustration of the relationship between migrant (mig.) and resident (res.) sex ratios and the proportion of migrants and residents in the population. In each of the three cases, the juvenile sex ratio is 1:1 (male:female) and the migrant sex ratio is female biased (a sex ratio of 1:3). However, as the relative proportion of migrants and residents changes, the resident sex ratio ranges between slightly male biased (a ratio of 3:2) to extremely male biased (a ratio of 9:1). The migrant and resident sex ratios mirror each other only when the proportion of migrants and residents is equal (50%).

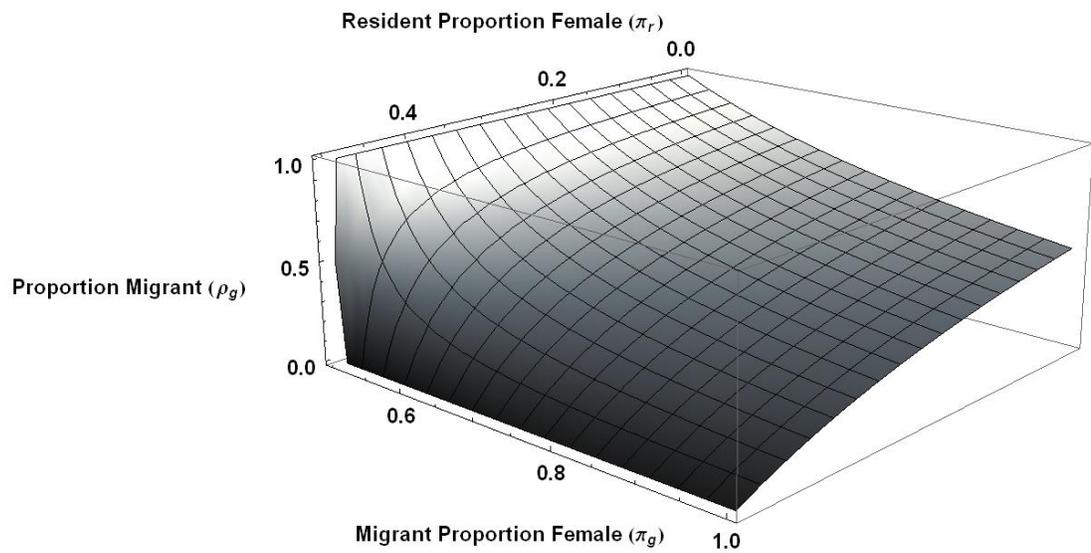


Figure 4.2: The relationship between the proportion of migrants and sex ratios in the migrant and resident groups (equation 4.2). This surface is limited to the case of female-biased migrants and male-biased residents.

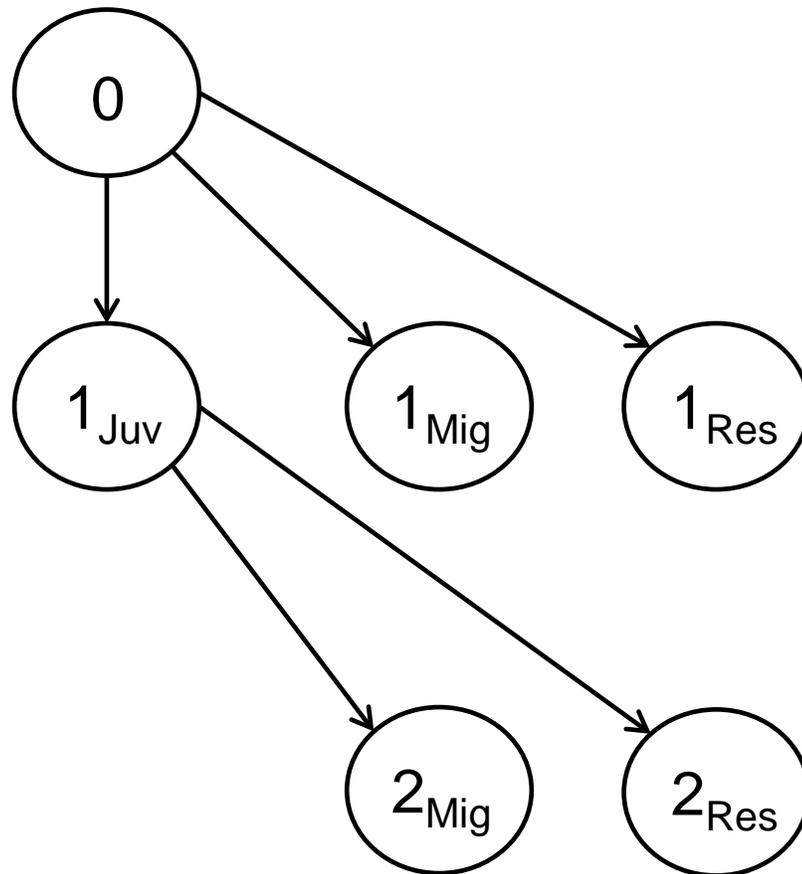


Figure 4.3: A life cycle diagram for the two age model example. In the first year, individuals can transition to a migrant or resident life history, or remain as juveniles. In the second year all remaining juveniles must transition to a migrant or resident life history. In this example, individuals are semelparous and cannot switch between life history types.

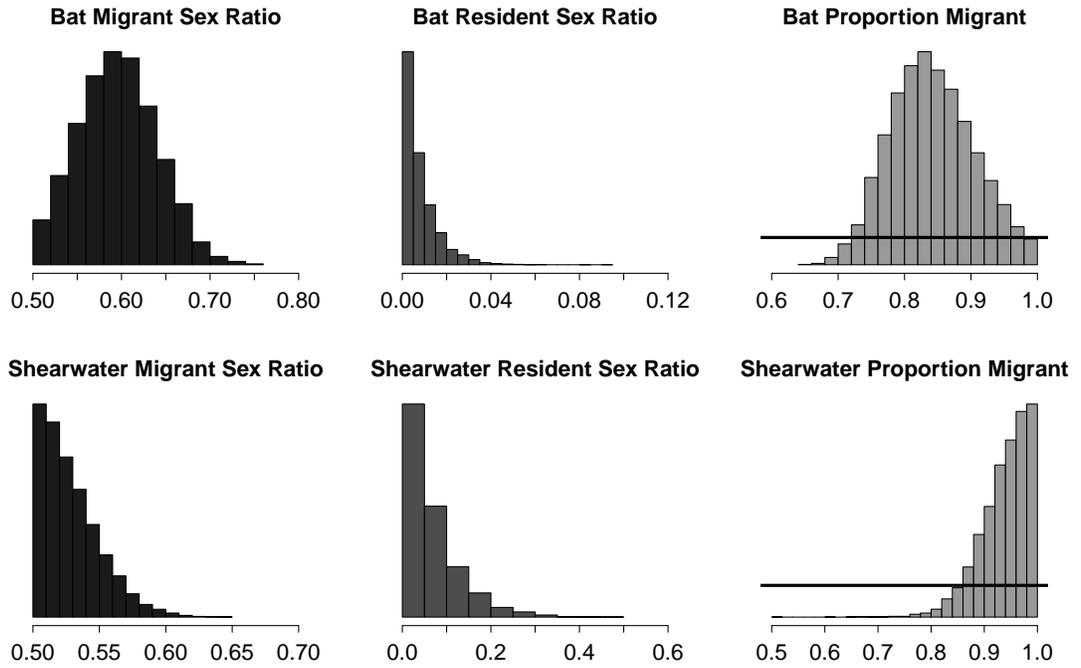


Figure 4.4: The posterior distributions of the migrant sex ratio, resident sex ratio, and proportion of migrants for (A) Daubenton's bats and (B) Cory's Shearwaters. The red line indicates the 95% HPD interval boundary. The sex ratio posterior distributions are bounded by their priors in order to limit the proportion migrant posterior estimate to between 0 and 1.

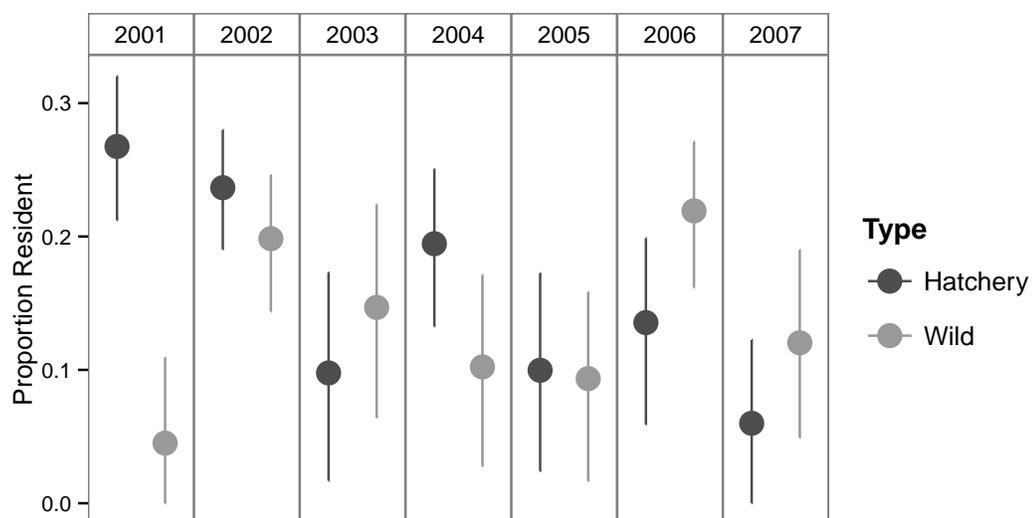


Figure 4.5: The calculated proportion of residents in wild and hatchery Chinook salmon from 2001 to 2007 in the Yakima River, USA. Error bars represent 95% HPD intervals. The sex ratio data used in this analysis was collected by Larsen et al. (2013).

Chapter 5 Conclusion

At the start of my dissertation, I posed the question of natural selection maintains phenotypic variation, such as partial migration. My results demonstrate that density-dependent competition is sufficient for the maintenance of partial migration, because it can lead to frequency-dependent fitness and balancing selection. This has important implications for predicting species' responses to future changes. Specifically, the predicted responses I observed were non-linear, meaning responses will vary depending on their initial value. To measure these predicted responses, I developed the method sex-ratio balancing, which estimates the propensity of migration based on sex ratios. This method could enable greater data collection on migration propensities and test theory on how natural selection maintains phenotypic variation.

I will end by saying that studying the details of natural selection is not just a theoretical exercise, it is the only way we can predict how organisms may adapt to their rapidly changing environments. Most species have diverse life histories and traits, and if we do not understand how this diversity is maintained, we have no chance of accurately predicting how they will, or will not, adapt. My hope is that my dissertation adds a small drop into the larger pool of research on natural selection, evolution, and ecology.

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APPENDIX

Chapter A Analysis of the results in Chapter 2

Anushaya Mohapatra and Patrick De Leenheer did this analysis and wrote up the following mathematical proof of the results. They start with the prior residence form of density dependence.

Rewriting the uncoupled system (3.4) as

$$x(t+1) = A_1(x(t), \phi)x(t), \quad (\text{A.1})$$

where

$$A_1(x, \phi) = \begin{pmatrix} 0 & f_M(x_M + x_N) & f_N(x_N) \\ \phi s_M & 0 & 0 \\ (1 - \phi)s_N & 0 & 0 \end{pmatrix} \text{ and } x = \begin{pmatrix} x_1 \\ x_M \\ x_N \end{pmatrix}$$

When $\phi \neq 0$ and $\phi \neq 1$, this model has an important invariance property:

$$\frac{x_N(t)}{x_M(t)} = \frac{(1 - \phi)s_N}{\phi s_M} =: c_1(\phi) = c_1, \text{ for all } t = 1, 2, \dots \quad (\text{A.2})$$

This means that the ratio of x_N and x_M is equal to the positive constant c_1 from time $t = 1$ onwards. In other words, all orbits reach the line $x_N/x_M = c_1$ in 1 time step, and remain there forever after. Thus, the system reduces to a planar system,

whose asymptotic behavior can be determined:

$$\begin{pmatrix} x_1(t+1) \\ x_M(t+1) \end{pmatrix} = \begin{pmatrix} 0 & f_M(d_1 x_M) + c_1 f_N(c_1 x_N) \\ \phi s_M & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_M(t) \end{pmatrix} \quad (\text{A.3})$$

Where $d_1 = c_1 + 1$. Note that since the functions g_M and g_N are increasing. Thus, systems (A.3) is monotone, and it has a positive fixed point $x^*(\phi) = (x_1^*, x_M^*)$ which follows from De Leenheer et al. (2017).

The coupled model is:

$$\begin{pmatrix} x_1(t+1) \\ x_M(t+1) \\ y_1(t+1) \\ y_M(t+1) \end{pmatrix} = \begin{pmatrix} A_1(x(t) + y(t), \phi) & & & 0 \\ & & & 0 \\ & 0 & & A_1(x(t) + y(t), \phi') \\ & & & \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_M(t) \\ y_1(t) \\ y_M(t) \end{pmatrix} \quad (\text{A.4})$$

or more explicitly,

$$x_1(t+1) = (f_M(d_1 x_M + d_2 y_M) + c_1 f_N(c_1 x_M + c_2 y_M)) x_M \quad (\text{A.5})$$

$$x_M(t+1) = \phi s_M x_1 \quad (\text{A.6})$$

$$y_1(t+1) = (f_M(d_1 x_M + d_2 y_M) + c_2 f_N(c_1 x_M + c_2 y_M)) y_M \quad (\text{A.7})$$

$$y_M(t+1) = \phi' s_N y_1 \quad (\text{A.8})$$

where

$$\begin{aligned} c_2 &= \frac{(1 - \phi')s_N}{\phi' s_M} \\ d_2 &= 1 + c_2 \end{aligned}$$

The system (A.4) has a fixed point at $X^*(\phi) = (x_1^*, x_M^*, 0, 0)$. From the PIP (figure 2.3), it is clear that in case of $\hat{x}_M > \tilde{x}_N$, $\phi^* = \frac{\frac{s_N}{\tilde{x}_M - 1} + \frac{s_M}{s_N}}{\frac{\tilde{x}_M}{\tilde{x}_N} - 1 + \frac{s_M}{s_N}}$ is the only candidate for ESS. To prove, it is in fact an ESS we perform a nonlinear stability analysis. We use following mathematical definitions.

Definition A.0.1 *We say that ϕ^* in $[0, 1]$ is an evolutionary stable strategy (ESS) if $X^*(\phi^*)$ is a locally asymptotically stable fixed point of system (A.4) for all $\phi' \neq \phi^*$ in some neighborhood of ϕ^* .*

This notion captures that if the resident population has adopted an ESS, then it cannot be invaded by mutants that use nearby strategies.

Definition A.0.2 *We say that ϕ^* in $[0, 1]$ is a convergence stable strategy (CSS) if there is a neighborhood N of ϕ^* such that $X^*(\phi^*)$ is not an asymptotically stable fixed point of system (A.4) for all pairs (ϕ, ϕ') with ϕ in N that satisfy that either $\phi < \phi' < \phi^*$ or $\phi^* < \phi' < \phi$, but an asymptotically stable fixed point of system (A.4) for all pairs (ϕ, ϕ') with ϕ in N that satisfy that either $\phi' < \phi < \phi^*$ or $\phi^* < \phi < \phi'$.*

Nonlinear stability analysis when $\hat{x}_M > \tilde{x}_N$ holds

By means of the linear coordinate change

$$\tilde{X} = X - X^*(\phi^*),$$

we first translate the fixed point $X^*(\phi^*)$ of the K -monotone system (A.5) to the origin of R^4 , and dropping tildes, we re-write the transformed system, which is also K -monotone, as

$$X(t+1) = F(X(t)). \tag{A.9}$$

We claim that as long as $\phi^* \neq \phi' \in (0, 1)$, the origin is an asymptotically stable fixed point for (A.9) with respect to perturbations $\Delta X = (\Delta x, \Delta y)$ near $X = 0$ for which Δx is arbitrary, but for which $\Delta y \geq 0$. We shall first show that there are two vectors $u_1 \leq_K 0$ and $0 \leq_K u_2$, such that the set $N = \{X \mid u_1 \leq_K X \leq_K u_2\}$ is a compact neighborhood of $X = 0$, and such that

$$u_1 \leq_K F(u_1) \leq_K 0 \leq_K F(u_2) \leq_K u_2. \tag{A.10}$$

To establish this claim, we first recall that Jacobian matrix $L(\phi^*, \phi')$ of $F(X)$ at $X = 0$ has eigenvalues L_{11} (which belongs to $(0, 1)$) and L_{22} (which equals 1 since $W(\phi^*, \phi') = 1$). By the Perron-Frobenius Theorem for K -monotone matrices (Vandergraft 1968), there exists an eigenvector $0 \leq_K V$ corresponding to the dominant

eigenvalue 1. In fact, this eigenvector can be calculated explicitly, yielding:

$$V = \begin{pmatrix} -\frac{(d_2 f'_M + c_1 c_2 f'_N) \phi'}{\phi(d_1 f'_M + c_1^2 f'_N)} \\ -\frac{(d_2 f'_M + c_1 c_2 f'_N) \phi' s_M}{(d_1 f'_M + c_1^2 f'_N)} \\ 1 \\ \phi' s_M \end{pmatrix}$$

where we have dropped the arguments $d_1 x_M^*$ and $c_1 x_M^*$ of the derivatives f'_M and f'_N respectively, to economize on our notation. Note that V belongs to the interior of K for all $\phi' \in (0, 1)$. We now show that for all sufficiently small $\epsilon > 0$, there holds that $u_1 \leq_K F(u_1)$, when $u_1 = -\epsilon V$.

By using a Taylor expansion for F near $X = 0$,

$$F(u_1) = L(\phi^*, \phi') u_1 + h(u_1) + O(\|u_1\|^3) = u_1 + h(u_1) + O(\|u_1\|^3). \quad (\text{A.11})$$

Here, $h = (h_1, h_2, h_3, h_4)^T$ with each $h_i(u_1) = u_1^T H_i u_1$ and H_i being the Hessian with respect to F_i . We have $h_2 = h_4 = 0$. We focus on finding the sign of $h_1(u_1)$ and $h_3(u_1)$.

We start by calculating $h_1(u_1) = u_1^T H_1 u_1$ where H_1 is the Hessian corresponding to F_1 . The reduced Hessian after dropping the zeros:

$$H_1^{red} = \begin{pmatrix} (H_1)_{22} & (H_1)_{24} \\ (H_1)_{24} & (H_1)_{44} \end{pmatrix}$$

where

$$\begin{aligned}(H_1)_{22} &= 2 \left(d_1 f'_M + c_1^2 f'_N \right) + x_M^* \left(d_1^2 f''_M + c_1^3 f''_N \right) \\(H_1)_{24} &= d_2 f'_M + c_1 c_2 f'_N + x_M^* \left(d_1 d_2 f''_M + c_1^2 c_2 f''_N \right) \\(H_1)_{44} &= x_M^* \left(d_2^2 f''_M + c_2^2 c_1 f''_N \right)\end{aligned}$$

We dropped the arguments $d_1 x_M^*$ and $c_1 x_M^*$ of the derivatives f'_M, f''_M and f'_N, f''_N respectively, to economize on our notation through out. A tedious calculation shows that $h_1(u_1) = u_1^T H_1 u_1 = ((u_1)_2, (u_1)_4) H_1^{red} \begin{pmatrix} (u_1)_2 \\ (u_1)_4 \end{pmatrix}$ can be simplified to:

$$h_1(u_1) = \frac{x_M^* (\phi' s_M)^2}{(d_1 f'_M + c_1^2 f'_N)^2} [(d_1 c_1 c_2 - d_2 c_1^2)^2 f''_M (f'_N)^2 + c_1 (c_1 d_2 - c_2 d_1)^2 f''_N (f'_M)^2]$$

Recall that $f'_M > 0, f'_N > 0$ and that $f''_M > 0, f''_N > 0$, and that $\phi^*, \phi' \in (0, 1)$ with $\phi' \neq \phi^*$. Moreover, $d_1 c_1 c_2 - d_2 c_1^2 \neq 0$ and $c_1 d_2 - c_2 d_1 \neq 0$. These facts imply that $h_1(u_1) > 0$, as claimed.

Similarly, $h_3(u_1) = u_1^T H_2 u_1$, where the reduced Hessian takes the form

$$H_3^{red} = \begin{pmatrix} (H_3)_{22} & (H_3)_{24} \\ (H_3)_{24} & (H_3)_{44} \end{pmatrix}$$

where

$$\begin{aligned}(H_3)_{22} &= 0 \\(H_3)_{12} &= d_1 f'_M + c_1 c_2 f'_N \\(H_3)_{22} &= 2 \left(d_2 f'_M + c_2^2 f'_N \right)\end{aligned}$$

Another tedious calculation shows that $h_3(u_1)$ can be simplified to:

$$\begin{aligned}h_3(u_1) = u_1^T H_3 u_1 &= ((u_1)_2, (u_1)_4) H_3^{red} \begin{pmatrix} (u_1)_2 \\ (u_1)_4 \end{pmatrix} \\ &= 2 \frac{(\phi' s_M)^2}{d_1 f'_M + c_1^2 f'_N} (c_1 - c_2)^2 f'_M f'_N\end{aligned}$$

Using the facts that $f'_M, f'_N < 0$ and $c_1 - c_2 \neq 0$, we have $h_2(u_1) < 0$, as claimed.

The existence of a vector $0 \leq_K u_2$ such that $F(u_2) \leq_K u_2$ can be established as follows. We reconsider system (A.9) with $\phi = \phi^*$, and fixed, but arbitrary

$\phi' \in (0, 1)$. Then the set $\{X = \begin{pmatrix} x_1 \\ x_M \\ y_1 \\ y_M \end{pmatrix} \mid y_1 = y_M = 0\}$ is invariant, and the

restriction of the monotone dynamics to this invariant set, is such that all solutions with positive initial x -component, converge monotonically to $x^*(\phi^*)$. Thus, there exists a positive vector b such that $0 \leq T(b) \leq b$ in R^2 , where $T(x)$ is the map on

the right-hand side of equation (A.3) with $\phi = \phi^*$. Consequently, by setting

$$u_2 = \begin{pmatrix} b - x^*(\phi^*) \\ 0 \end{pmatrix},$$

it follows that $u_2 \geq_K 0$, and it can be verified that

$$F(u_2) = \begin{pmatrix} T(b) - x^*(\phi^*) \\ 0 \end{pmatrix} \leq_K \begin{pmatrix} b - x^*(\phi^*) \\ 0 \end{pmatrix} = u_2$$

Combining the existence of the vectors u_1 and u_2 with the properties listed above, and the fact that system (A.9) is K -monotone, establishes (A.10). Notice in particular that the vectors u_1 and u_2 are such that N is indeed a compact neighborhood of $X = 0$.

Now, since system (A.9) is K -monotone, (A.10) implies that the orbit starting at u_1 is increasing with respect to the partial order \leq_K , and bounded above (by the zero fixed point). Thus, it must converge to some fixed point X_1 in N . Similarly, K -monotonicity and (A.10) imply that the orbit starting in u_2 is decreasing with respect to the partial order \leq_K , and bounded below by the zero fixed point, and must also converge to some fixed point X_2 in N . We now claim that we can always shrink N by choosing $\epsilon > 0$ sufficiently small in the definition of u_1 , so that $X_1 = X_2 = 0$. Suppose that $(\tilde{x}_1, \tilde{x}_M, \tilde{y}_1, \tilde{y}_M)$ is any fixed point of system (A.9) in N , with $\tilde{y}_M, \tilde{y}_1 \geq 0$. If $\tilde{y}_M = 0$ or $\tilde{y}_1 = 0$, we first shrink N by choosing $\epsilon > 0$ sufficiently small in the definition of the vector u_1 , so that N

does not include the fixed point $(-x^*(\phi^*), 0)$ of system (A.9). Then \tilde{x}_1 and \tilde{x}_M must also be equal to 0 since $(0, 0, 0, 0)$ is the unique fixed point in N of system (A.9) restricted to the invariant set where $y_M = y_1 = 0$. Therefore, any fixed point $(\tilde{x}_1, \tilde{x}_M, \tilde{y}_1, \tilde{y}_M)$ in N is necessarily such that $\tilde{y}_M, \tilde{y}_1 \neq 0$. Thus, $(\tilde{y}_M, \tilde{y}_1)$ must necessarily be positive vector because $\phi' \in (0, 1)$. Moreover, as shown above, for any fixed point $\tilde{x} = (\tilde{x}_1, \tilde{x}_M, \tilde{y}_1, \tilde{y}_M)$ in N , we have made sure that $\tilde{x} + x^*(\phi^*)$ is a positive as well. Therefore, if N would contain a fixed point \tilde{x} , other than $X = 0$, then both $\tilde{x} + x^*(\phi^*)$ and \tilde{x} would be positive. Then the original system (A.4) would have a positive fixed point as well which is not true, as we prove the system (A.4) can have at most one positive fixed point when $\phi = \phi^*$ and $\phi' \neq \phi^*$ as follows.

Let $(\tilde{x}_1, \tilde{x}_M, \tilde{y}_1, \tilde{y}_M)$ be a positive fixed point of (A.4)

If we set

$$z_1 = d_1\tilde{x}_M + d_2\tilde{y}_M \quad (\text{A.12})$$

$$z_N = c_1\tilde{x}_M + c_2\tilde{y}_M \quad (\text{A.13})$$

then there must hold in particular, that:

$$\begin{pmatrix} s_M\phi^* & c_1s_M\phi^* \\ s_M\phi' & c_2s_M\phi' \end{pmatrix} \begin{pmatrix} f_M(z_1) \\ f_N(z_2) \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \quad (\text{A.14})$$

Let $B = \begin{pmatrix} s_M \phi^* & c_1 s_M \phi^* \\ s_M \phi' & c_2 s_M \phi' \end{pmatrix}$, and notice that $\det(B) = s_M s_N (\phi^* - \phi') \neq 0$ since $\phi' \neq \phi^*$. Hence, the system (A.14) can have at most one solution (z_1, z_2) because both functions f_M and f_N are decreasing, and are therefore 1-to-1 functions. Equations (A.12) – (A.13) can be re-written as follows:

$$\begin{pmatrix} d_1 & d_2 \\ c_1 & c_2 \end{pmatrix} \begin{pmatrix} \tilde{x}_M \\ \tilde{y}_M \end{pmatrix} = \begin{pmatrix} z_1 \\ z_2 \end{pmatrix} \quad (\text{A.15})$$

Similarly, (A.15) has at most one solution $(\tilde{x}_M, \tilde{y}_M)$. Consequently, we have shown that the coupled system (A.4) can have at most one positive fixed point, as claimed.

By choosing $\epsilon > 0$ even smaller in the definition of u_1 , we can now ensure that the corresponding shifted fixed point for system (A.9), does not belong to N . Therefore, N is an isolating neighborhood for the fixed point $X = 0$, in the sense that it contains no other fixed points. In conclusion, we have proved the claim that $X_1 = X_2 = 0$ by appropriately choosing N , and therefore by K -monotonicity, all solutions in the compact, invariant neighborhood N , converge to $X = 0$. Going back to the original coordinates, we have proved that the fixed point $X^*(\phi^*)$ of the coupled system (A.4) is locally asymptotically stable, which completes the proof of the result.

Results for other forms of density dependence follow from this proof.

Sign of the W function and PIPs

1. Within phenotype.

We have $W(\phi, \phi') = 0$ if and only if $\phi = \phi'$ or $\phi = \phi^* = \frac{\hat{x}_M/\tilde{x}_N}{\hat{x}_M/\tilde{x}_N + s_M/s_N}$.

$W(\phi, \phi')$ is a continuous function, which is zero if and only if either the pair (ϕ, ϕ') belongs to the diagonal where $\phi = \phi'$, or to the vertical line through ϕ^* . These two lines divide the square $[0, 1] \times [0, 1]$ in four open regions, where the sign of the function W is either positive or negative. The sign of $W(\phi, \phi')$ for pairs (ϕ, ϕ') in the SE region in figure 2.3 is the same as the sign of $W(1, 0) = -(1 - s_N f_N(0))$, which is positive as $s_N f_N(0) > 1$. Similarly, $W(0, 1) = s_M f_M(0) - 1$ is positive as $s_M f_M(0) > 1$, and thus $W(\phi, \phi') > 0$ in the NW region. The sign of $W(\phi, \phi')$ for pairs (ϕ, ϕ') in the NE region is the same as the sign of $W(\phi, 1)$, where ϕ is an arbitrary value in the open interval $(\phi^*, 1)$. The sign of $W(\phi, 1)$ is equal to the sign of the second factor $s_M f_M(x_M^*(\phi)) - s_N f_N(x_N^*(\phi))$, which is continuous in ϕ and can only be zero when $\phi = \phi^*$. Since $\phi > \phi^*$, it follows that the sign of this second factor is equal to the sign of $s_M f_M(x_M^*(1)) - s_N f_N(x_N^*(1)) = 1 - s_N f_N(0)$, which is negative. Thus, $W(\phi, \phi')$ is negative for all pairs (ϕ, ϕ') in the NE region. A similar argument shows that $W(\phi, \phi')$ is negative for all pairs (ϕ, ϕ') in the SW region.

2. Between phenotype.

When $\hat{x}_M < \tilde{x}_N$, we have $W(0, 1) = s_M f_M(\tilde{x}_N) - 1 < 0$, and $W(1, 0) = s_N f_N(\hat{x}_M) - 1 > 0$.

If $\hat{x}_M > \tilde{x}_N$, we get $W(0, 1) = s_M f_M(\tilde{x}_N) - 1 > 0$ and $W(1, 0) = s_N f_N(\hat{x}_M) - 1 < 0$.

Using continuity of $W(\phi, \phi')$, we have the PIP's as in figure 2.3.

3. Prior resident.

When $\hat{x}_M > \tilde{x}_N$, it turns out that $W(\phi, \phi') = 0$ iff $\phi = \phi'$ or $\phi = \phi^*$ where $\phi^* = \frac{\frac{s_N}{\tilde{x}_N - 1} + \frac{s_M}{\hat{x}_M - 1}}{\frac{s_N}{\tilde{x}_N - 1} + \frac{s_M}{\hat{x}_M - 1}}$ and PIP is similar to within phenotype (figure 2.3).

When $\hat{x}_M < \tilde{x}_N$, $W(\phi, \phi') = 0$ iff $\phi = \phi'$. And $W(0, 1) = s_M f_M(\tilde{x}_N) - 1 < 0$ and $W(1, 0) = s_N f_N(0) - s_M f_M(\hat{x}_M) > 1 - s_M f_M(\hat{x}_M) > 0$. So PIP in figure 2.3 follows from continuity of W function.

4. Migrant advantage.

This case is analogous to that of prior residency with reverses the role of migrants and non-migrants.

