CHAPTER 3

Theoretical reflections on the evolution of migration

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Table of contents

3.1 **Introduction** 17
3.2 **An idealized organism in an idealized world** 17
3.3 **When is a non-migratory species vulnerable to invasion by migratory strategies?** 18
3.4 **When is a migratory species vulnerable to invasion by non-migratory strategies?** 22
3.5 **Discussion** 27

3.1 Introduction

Migration in nature occurs against a complex, shifting backdrop of kaleidoscopic changes through time due to many distinct forces of variation acting over different time scales, from stochastic daily fluctuations in the weather, to multi-annual oscillations in the abundance of resources and natural enemy populations, to the stately march of climate change over geological time. Migrants move across landscapes that are complex over many spatial scales (Chapter 7). Organisms themselves are of course comparably complex, with plastic, multifaceted adaptive strategies for contending with variation in the environment across space and time (Chapter 2).

The theoretical fitness consequences of migration have been considered many times and in many ways. Most of these models, however, have been built around specific taxa or ecosystems. To gain a conceptual handle on the evolutionary forces that have generated and today maintain migration, we suggest it might be equally useful to start with a simple idealized organism living in an equally idealized world. Here we consider the conditions under which non-migratory home range behaviour is vulnerable to invasion by a migratory phenotype; we also consider the converse conditions under which a migratory population can be invaded by non-migratory individuals. Our larger goals are to clarify the logic underlying migratory habitat selection in a seasonal environment, help to define conditions for what we might call the 'evolutionary statics' of migration, and set the stage for more complex evolutionarily dynamic models. At the end of this chapter, we will consider how our simple model compares with other models of the evolution of migration in the published literature.

3.2 An idealized organism in an idealized world

The organism we consider is one that has haploid or clonal inheritance with no age or stage structure. It lives in a world with two distinct habitats, and two distinct seasons in each habitat, but no inter-annual variability. The model is deterministic, and so we

are ignoring the impact of both environmental and demographic stochasticity. Within a given habitat type, all individuals are assumed to have the same fitness. Genetic variation, if present, influences the propensity to move between the two habitats, but not fitness within each habitat. We follow the usual protocol of analyses of evolutionary stability and adaptive dynamics, which is to assume that initially the species is fixed for one strategy (i.e., one clone), and then ask if this strategy can be invaded by another, rare clone. The habitats are assumed to be far enough apart that an imposed perturbation in population density in one habitat does not at the same time alter the fitnesses of the individuals in the other habitat. In other words, density dependence, if it occurs, is entirely within-habitat.

Our measure of 'fitness' is very simple. If, in the absence of movement, at the start of an annual cycle in generation t there are $N(t)$ individuals of a given clone in habitat i (i = A,B), and at the end of season 1, of length τ, there are $N(t + \tau)$ present, then average 'seasonal fitness' is measured as the per capita contribution of each individual (including itself) to the population present at $t + \tau$, or

$$R_{i1} = \frac{N(t+\tau)}{N(t)}.$$

Likewise, for each individual present at the beginning of season 2, of length $1 - \tau$, the expected number it will leave to start the next generation, $t + 1$, (its seasonal fitness for this second season) is

$$R_{i2} = \frac{N(t+1)}{N(t+\tau)}.$$

The fitness over a complete annual cycle in habitat i is the multiple of these:

$$F_{Tannual} = R_{i2}R_{i1} = \frac{N(t+1)}{N(t)},$$

the usual measure of fitness for an organism with discrete generations synchronized to an annual cycle. What we have done is express overall annual fitness as a product of what we are calling 'seasonal fitnesses'. The proposition that we will explore is that the patterning of seasonal fitnesses can be examined to characterize when non-migration and complete migration are respectively evolutionarily stable strategies, or ESSs for short (Maynard-Smith 1982).

We can generalize this approach to consider two habitats, where R_{ij} denotes the seasonal fitness of an individual in habitat i during season j. Any of these seasonal fitnesses can be functions of density. Over any given generation, the system is thus defined by four seasonal fitnesses (two seasons in each of habitats A and B). In this snapshot, there are four combinations of seasonal fitnesses possible over an annual cycle ($R_{A1}R_{A2}$, $R_{B1}R_{B2}$ $R_{A1}R_{B2}$, and $R_{B1}R_{A2}$). The first pair of annual fitnesses describes individuals who stay in either habitat over the annual cycle, whereas the second pair pertains to individuals who migrate, in each of the two possible directions (habitat A to B versus habitat B to A), over a given year.

We are here interested in populations that persist and are naturally regulated by density dependence occurring somewhere in the life cycle, in at least one habitat at one season. We assume that our initial population is genetically homogeneous and in demographic equilibrium. Our general models make no specific assumptions about density dependence, except making the implicit assumption that it occurs, and that the population is initially at its demographic equilibrium. When we use a specific model to provide some numerical examples to accompany the analytical results, for simplicity we assume that density dependence is in a single season. Future work should extend such specific models to incorporate density dependence across both seasons.

3.3 When is a non-migratory species vulnerable to invasion by migratory strategies?

We first start with a population that is non-migratory, and ask if a migratory strategy can colonize. For non-migration to be in equilibrium, without loss of generality we can assume that the initial habitat occupied is habitat A. In other words, for this case, the initial condition is for the species to occupy a restricted geographical range, within which seasonal variation occurs. When is this restricted distribution an ESS, relative to a rare invasive migratory strategy? We assume for now that there are no costs to movement (this is, of course, a huge assumption).

For the non-migratory specialist in habitat A to be in demographic equilibrium requires $R_{A1}R_{A2} = 1$,

hence the 'rate' of geometric growth must be unity. We will denote fitness at population equilibrium by asterisks (R_{A1}*R_{A2}*). If an individual moves to habitat B, and stays there (i.e., a rare dispersal event, rather than migration), for the initial condition to persist (and thus for the restricted range to be ecologically stable) it requires that

$$R^*_{A1}R^*_{A2} > R_{B1}R_{B2} \quad \text{or} \quad 1 > R_{B1}R_{B2}. \tag{1}$$

This simply restates the fact that, in a closed population, there is a geometric growth rate criterion for population persistence.

If now a mutant individual arises that regularly shuttles back and forth between the two habitats, it can experience two possible net growth rates, depending upon the order of seasons it experiences. For non-migration to be an ESS (i.e., a rare migratory clone which attempts to invade, and migrates completely between the two habitats within each year, then declines towards extinction), we must have both

$$R^*_{A1}R^*_{A2} > R^*_{A1}R_{B2} \quad \text{and} \quad R^*_{A1}R^*_{A2} > R_{B1}R^*_{A2}.$$

The fact that there are two conditions reflects the fact that there are logically two distinct patterns of complete migration between two habitats. Based on our assumption of demographic equilibrium for the resident population, this pair of inequalities simplifies to

$$1 > R^*_{A1}R_{B2} \quad \text{and} \quad 1 > R_{B1}R^*_{A2}.$$

Without loss of generality, assume season 2 in habitat A is the bad season. Because $R^*_{A1}R^*_{A2}=1$, we can eliminate R^*_{A1} from our equation by letting $R^*_{A1} = 1/R^*_{A2}$ So, the conditions for non-migration to be an ESS are:

$$1 > (1/R^*_{A2})R_{B2} \quad \text{or} \quad R^*_{A2} > R_{B2}, \quad \text{and}$$
$$1 > R_{B1}R^*_{A2} \quad \text{or} \quad 1/R_{B1} > R^*_{A2}.$$

We can put these two inequalities together in a joint inequality, defining the necessary and sufficient demographic conditions for non-migration to be an ESS, as follows:

$$1/R_{B1} > R^*_{A2} > R_{B2}. \tag{2}$$

Note that Equation 2 implies Equation 1, which was earlier deduced to be the condition for ecological stability of habitat specialization (to habitat A) in a seasonal world. So a necessary condition for non-migration to be an ESS, with specialization to habitat A, is that colonization of habitat B (without back-migration) fails.

But this is not sufficient. In other words, there can be habitats that cannot sustain a population, on their own, but which could foster the evolution of migration. In particular, if $R_{A2}^* < R_{B2}$, then the non-migratory condition is not an ESS, and complete migration can invade. Put simply, if the seasonal fitness during the worst season in the habitat initially occupied (habitat A) is less than seasonal fitness in the other unoccupied habitat (habitat B), an individual that begins a migratory shuttle between habitats, leaving habitat B after season 2 then back to habitat A for season 1, enjoys the best of both, and can invade. A comparable condition arises in analyses of the utilization of stable sink habitats when source habitats fluctuate in fitness, as part of spatial bet-hedging strategies (Holt 1997).

If the necessary condition in Equation 1 does not hold, then habitat 2 should be colonized. In the continued absence of migration, each habitat should then equilibrate over time such that its geometric mean fitness is unity, or

$$1 = R^*_{A1}R^*_{A2} \qquad \text{and} \qquad 1 = R^*_{B1}R^*_{B2}. \tag{3}$$

We have now added asterisks to the seasonal fitnesses in habitat B to denote the requirement for population equilibration. The reason is that after invasion of habitat B, numbers must grow there until density dependence occurs, such that fitness over the annual cycle is unity. This requires that one or both seasonal fitnesses must be functions of density, so realized seasonal fitness for at least one season at equilibrium is depressed over the initial seasonal fitness at the time of invasion.

Is this distribution, where a species occupies two habitats but does not migrate between them, stable against invasion by a completely migratory genotype? As a limiting case, we assume that there is no cost to such migration. The migratory genotype has two possible fitnesses, depending upon its order of movement during the annual cycle.

$$R^*_{A1}R^*_{B2} \quad \text{or} \quad R^*_{B1}R^*_{A2}.$$

For both of these to be less fit than the resident non-migratory type requires that both

$$R^*_{A1}R^*_{B2} < 1 \quad \text{and} \quad R^*_{B1}R^*_{A2} < 1. \tag{4}$$

Again, we can use the assumption of demographic equilibrium to eliminate some terms. At demographic equilibrium in the non-migratory population,

$$R^*_{A2} = 1 / R^*_{A1} \quad \text{and} \quad R^*_{B2} = 1 / R^*_{B1}. \tag{5}$$

Substituting the left-hand equality of (5) into the right inequality of (4) leads to

$$R^*_{B1} < R^*_{A1}. \tag{6}$$

Substituting the right-hand equality of (5) into the left inequality of (4) R_{B2}* gives

$$R^*_{B1} > R^*_{A1}. \tag{7}$$

Inequalities (6) and (7) are contradictory.

Ergo, the above line of reasoning thus leads to the simple conclusion that:

> *If a species can persist across two habitats without movement between them, and those two habitats fluctuate through time, in a manner that is reflected in 'seasonal fitness', then the species is always vulnerable to invasion by a completely migratory genotype.*

The migratory strategy in effect exploits the fact that in each habitat, there is a season where seasonal fitness is greater than one (a necessary consequence of temporal variation in fitness, combined with the assumption of demographic equilibrium in each habitat). Shuttling regularly between habitats, when rare, then clearly implies an initial geometric mean fitness greater than one. Interestingly, this may hold even if it implies that the migratory type (which we recall is rare) moves into a habitat during the season when seasonal fitness there is lower than in the alternate season, and the two habitats experience synchronous and in-phase variation in seasonal fitnesses.

A numerical example may suffice to illustrate this point. For simplicity, we assume that density dependence occurs in the same season in each habitat, which is the time of year when a single bout of reproduction occurs, with no density dependence in the other season. Fitness in the birth season in both habitats is given by a Ricker formulation (1954), with density dependence arising from the summed density of all clones that are found in a given habitat. Fitness in the non-breeding season is determined by the magnitude of a density-independent rate of survival. We can represent morph dynamics with the following system of equations:

$$N1(t+1) = N1(t) \cdot \exp(r_A \cdot [1 - N1(t) - N3(t)] + s_A), \tag{8a}$$

$$N2(t+1) = N2(t) \cdot \exp(r_B \cdot [1 - N2(t) - N4(t)] + s_B), \tag{8b}$$

$$N3(t+1) = N3(t) \cdot \exp(r_A \cdot [1 - N1(t) - N3(t)] + s_B), \tag{8c}$$

$$N4(t+1) = N4(t) \cdot \exp(r_B \cdot [1 - N2(t) - N4(t)] + s_A), \tag{8d}$$

where $\exp(r_j)$ is the maximal birth rate of individuals in habitat j during the breeding season, $\exp(s_j)$ is the exponential survival rate of individuals in habitat j in the non-breeding season, and $Ni(t)$ is the population density of individuals of behavioural morph i at time t. In this formulation, morph 1 represents individuals that are selective for the best year-round habitat A; morph 2 represents individuals that are selective for the worst year-round habitat B; morph 3 represents individuals that reproduce in the best habitat, but migrate to the other habitat in the non-growing season (dubbed 'logical migrants'); and, morph 4 represents individuals that reproduce in the poorer habitat, but migrate to the other habitat in the non-growing season (labelled 'perverse migrants'). We have scaled density so that if survival is guaranteed through the non-breeding season, carrying capacity (viz., equilibrial density) is set at unity. Morphs that co-occur are competitively equivalent, as measured by density dependence in births.

This is perhaps the simplest mathematical representation possible for depicting seasonal migration, demarcating a period of density-dependent growth from a season of density-independent mortality, and contrasting the fates of clones that interact equivalently with each other but display different migratory propensities.

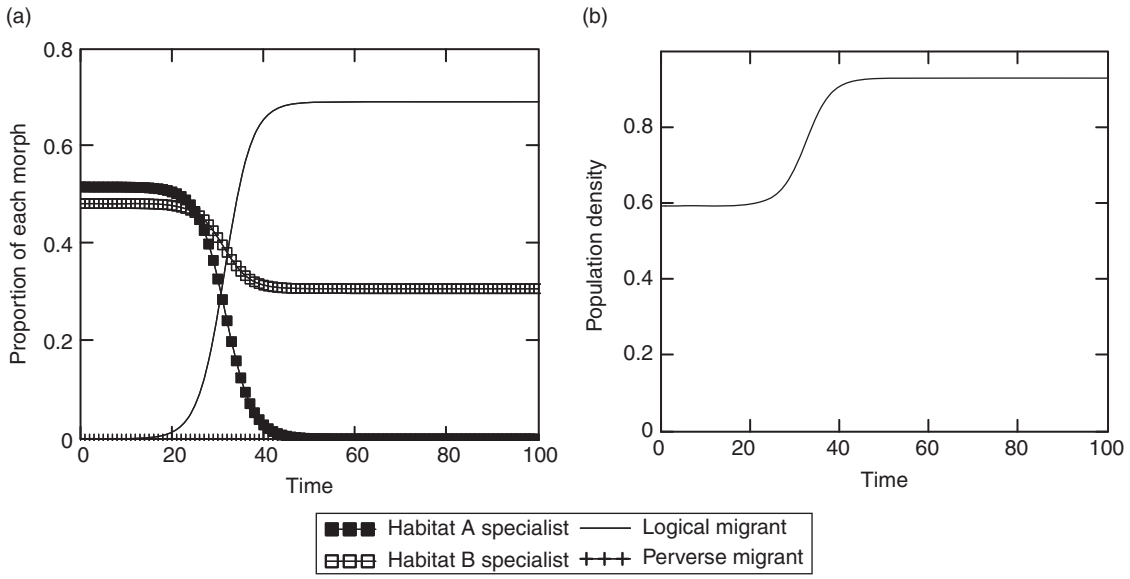

Figure 3.1 Variation over time in the relative frequency of (a) behavioural morphs and (b) total population abundance in a system with specialists in two distinct habitats that is invaded by rare morphs that migrate between habitats on a seasonal basis ($r_A = 1.0$, $r_B = 0.5$, $s_A = -0.69$, $s_B = -0.36$). Habitat A is best during the growing season, whereas habitat B is best during the non-growing season.

Fitness maxima (i.e. the per capita annual rate of change as $N \to 0$, which is equal to the product of the seasonal fitnesses) can be readily calculated as $R_{A1}\, R_{A2} = \exp(r_A + s_A)$ for sedentary (i.e., non-migratory) specialists in habitat A, $R_{B1}\, R_{B2} = \exp(r_B + s_B)$ for sedentary specialists in habitat B, $R_{A1}\, R_{B2} = \exp(r_A + s_B)$ for those migrants that use the best habitat to breed and $R_{B1}\, R_{A2} = \exp(r_B + s_A)$ for the perverse migrants that use the worst habitat to breed. For any of these four morphs, its maximal fitness must exceed unity, or it will surely disappear. In isolation, the equilibrium abundance of specialists in the best habitat = $1 + s_A/r_A$, whereas the equilibrium abundance of specialists in the worst habitat = $1 + s_B/r_B$. For these quantities to make sense (i.e., have a non-zero population) requires that $|s_i| < r_i$. We will assume that these general conditions for potential viability of each strategy hold.

Assume as an example that a non-migratory species occupies habitat A, where $r_A = 1$ and $s_A = -0.69$. These demographic parameters imply an equilibrium density of 0.31 (where $N_{eq} = 1 + s_A/r_A$). Seasonal fitness in habitat A fluctuates between $R_{A1} = \exp(r_A[1 - N_{eq}]) = 2$ in the growing season and $R_{A2} = \exp(s_A) = 0.5$ in the non-growing season. Fitness over the year is the product of these two numbers, 1, so the population in habitat A is in demographic equilibrium. A non-migratory population in habitat B, where $r_B = 0.5$ and $s_B = -0.36$, is in demographic equilibrium at a population density of 0.28 (where $N_{eq} = 1 + s_B/r_B$). While breeding success is lower at equilibrium in habitat B, such that $R_{B1} = \exp(r_B[1 - N_{eq}]) = 1.43$, animals residing there enjoy a more benign environment in the non-breeding season, such that $R_{B2} = \exp(s_B) = 0.7$. Good and bad seasons are synchronized across space. If a migratory genotype now arose, which resided in habitat A in the good season, and habitat B in the bad season, its annual growth rate when rare would be (2)(0.7) = 1.4, so it would be selected and increase when rare (Fig. 3.1).

In this example, one would expect to see the evolution of at least some migration into and out of the poorer habitat. Paradoxically, however, some individuals should leave just as conditions begin to improve locally in habitat A. In turn, the evolution of logical migration in this example makes it inevitable that non-migratory morphs would also persist in the poorer habitat, because their increase in the growing season more than compensates for

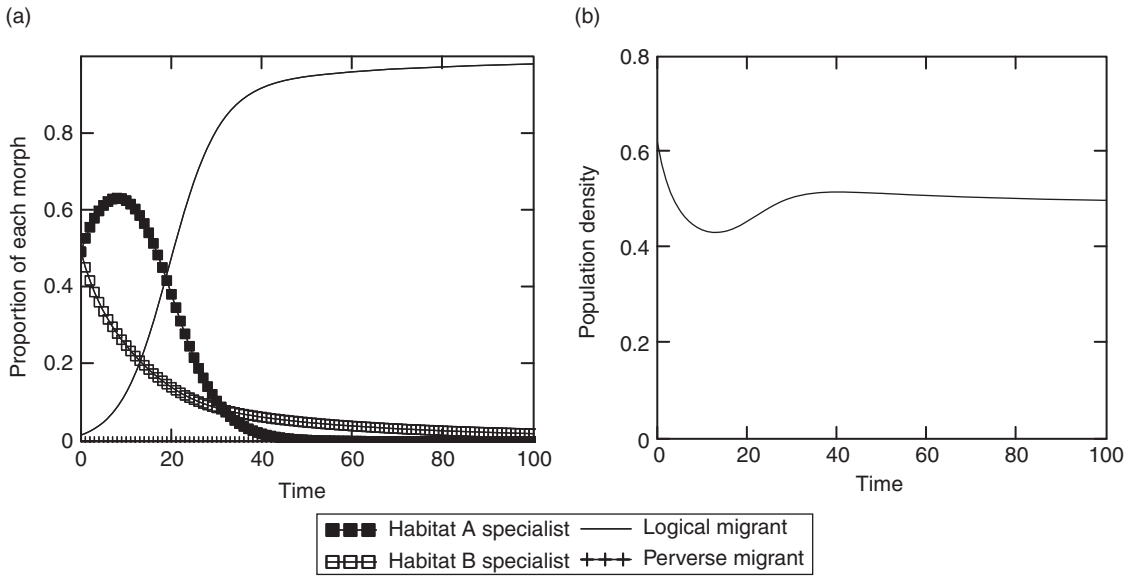

Figure 3.2 Variation over time in the relative frequency of (a) behavioural morphs and (b) population abundance in a system with specialists in two distinct habitats that is invaded by rare morphs that migrate between habitats on a seasonal basis ($r_A = 1.0$, $r_B = 0.5$, $s_A = -0.69$, $s_B = -0.51$). Habitat A is best during the growing season, whereas habitat B is best during the non-growing season. Unlike the system in Fig. 3.1, habitat B is a sink if occupied year-round. Initial abundance of both specialists is 0.31.

their density-independent losses during the non-growing season. This of course hinges on the assumption that the non-migrant can escape from any density-dependent effects experienced from the much larger resident population, when they co-occur during the non-growing season. If habitat B is a sink (were it to be occupied on a year-round basis) then only migrants can persist in the system (Fig. 3.2), echoing a pattern seen in earlier models of habitat-mediated dispersal (McPeek and Holt 1992; Holt 1997). Provided that the fitness in alternating habitats is high enough, it is readily possible to construct a system in which both habitats are sinks, yet permitting persistence of migrants, although such migrants could only arrive via colonization from elsewhere.

So far we have assumed that habitats alternate seasonally in terms of fitness advantage. This need not be the case, of course; habitat A might well yield both the higher rate of growth and the higher survival in the non-growing season. In this case, non-migratory individuals obviously would have an advantage over all other morphs and would predominate (Fig. 3.3). However, this situation opens an opportunity for a perverse migrant to evolve, one that chooses to breed in the poorer habitat, but then moves into the better habitat during the non-growing season. As before, this outcome may depend on our assumption of no competition during the non-growing season.

3.4 When is a migratory species vulnerable to invasion by non-migratory strategies?

We now start, in effect, at the other end of the spectrum of migratory behaviours, and assume that the species is initially completely migratory, thus abandoning each habitat in turn over the course of the annual cycle. When can this species be invaded by a completely non-migratory strategy? Another question that should be considered is whether this migratory strategy can be invaded by a counter-migratory strategy (i.e. individuals that go in the opposite direction to the general spatial flow of the population)?

To address these questions, we can assume that the initial condition is such that individuals use the

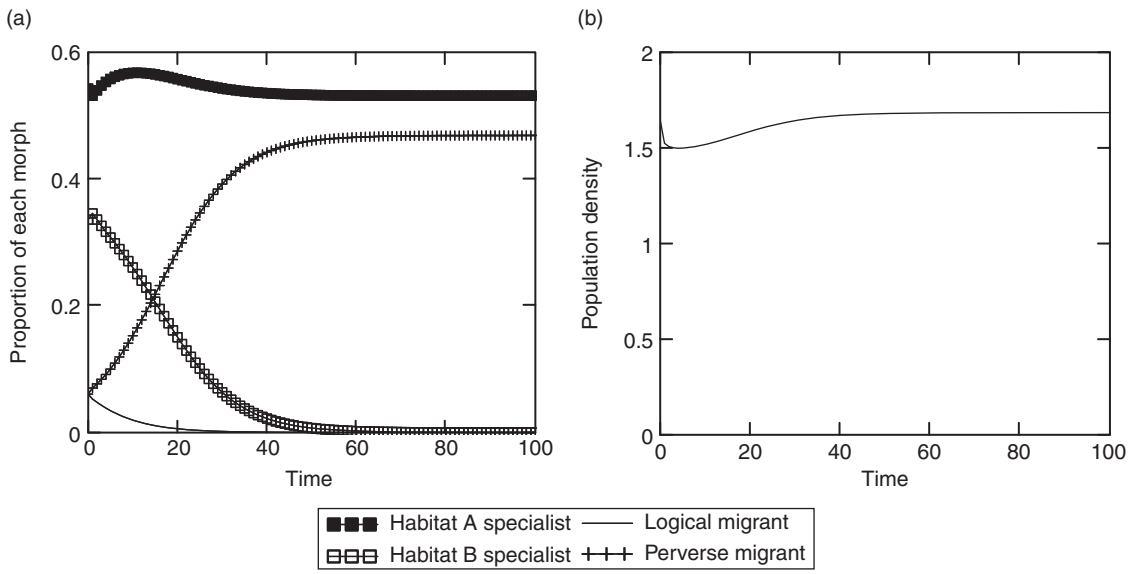

Figure 3.3 Variation over time in the relative frequency of (a) behavioural morphs and (b) population abundance in a system with specialists in two distinct habitats that is invaded by rare morphs that migrate between habitats on a seasonal basis ($r_A = 1.0$, $r_B = 0.5$, $s_A = -0.11$, $s_B = -0.22$). Habitat A is best in both seasons.

best habitat (A) in the breeding season, but migrate to the other habitat (B), during the non-breeding season. The realized annual fitness over this cycle (again ignoring the potential cost of movement itself) is

$$F_{migration} = R^*_{A1}R^*_{B2} = 1, \tag{9}$$

assuming demographic equilibrium (hence the use of asterisks). Because breeding occurs in A we can assume that

$$R^*_{A1} > 1 > R^*_{B2}. \tag{10}$$

If a few individuals stay behind in habitat A, or habitat B, respectively, they will experience little or no density dependence, and so have expected fitnesses of

$$F_1 = R^*_{A1}R_{A2} \quad \text{and} \quad F_2 = R_{B1}R^*_{B2}. \tag{11}$$

The asterisks indicate that in the respective seasons, there may be density dependence in that habitat. The absence of asterisks indicates that, in that season, there should be no density dependence, when a novel non-migratory clone is initially rare (because the migratory population has completely left that habitat, for the other one).

For complete migration to be an ESS, each of these fitnesses for non-migrants must be less than unity:

$$R^*_{A1}R_{A2} < 1 \quad \text{and} \quad R_{B1}R^*_{B2} < 1. \tag{12}$$

Multiplying these two inequalities together leads to

$$R^*_{A1}R_{A2}R^*_{B2}R_{B1} < 1. \tag{13}$$

Substituting (9) into (13), then

$$R_{B1}R_{A2} < 1. \tag{14}$$

The inequality in (14) represents the annual growth rate of a perverse migratory genotype, going in the opposite direction to the resident type, when it is initially rare and hence experiences no density dependence. So if non-migrants cannot invade (i.e., the conditions in (12) hold), then counter-migration is simply unviable.

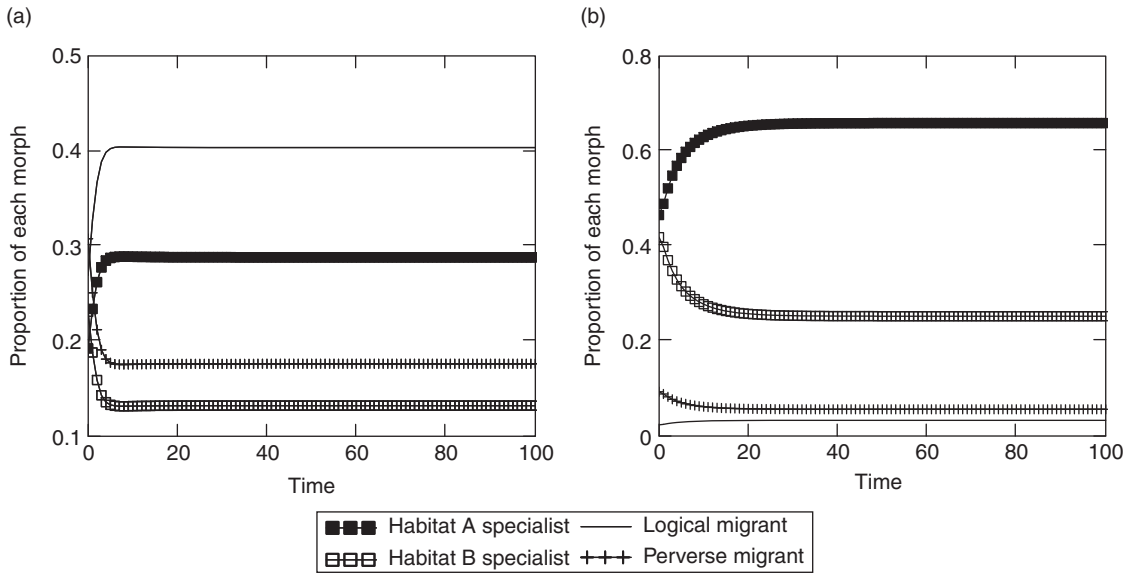

Figure 3.4 Variation over time in the relative frequency of behavioural morphs in a system with specialists in two distinct habitats that is invaded by rare morphs that migrate between habitats on a seasonal basis ($r_A = 1.0$, $r_B = 0.5$, $s_A = -0.36$, $s_B = -0.36$). Both habitats yield equal fitness in the non-growing season, although habitat 1 provides higher fitness in the growing season. The two sub-plots show simulations with differences in initial conditions: (a) population densities for both habitat specialists set initially at equilibria, (b) habitat specialist A was initiated at equilibrium, whereas habitat specialist B was initiated ~ 10% below its equilibrium. Migrants started lower in (b).

What about non-migration? We can re-write (12) as

$$R_{A2} < \frac{1}{R^*_{A1}} \quad \text{and} \quad R_{B1} < \frac{1}{R^*_{B2}}. \tag{15}$$

It is clear after substitution from (10) into the left side of (15) that a non-migratory strategy in the better habitat A is excluded, provided that seasonal fitness in the 'off'-season (when the migrants are elsewhere) is sufficiently less than unity.

Intriguingly, exclusion does not require low fitness in the poorer habitat B. Because R_{B2}*<1, it is possible for $R_{B1} > 1$, yet for a resident strategy remaining in habitat B nonetheless to be excluded. The reason is that even though seasonal fitness in the absence of migrants exceeds one in season 1, fitness averaged over the entire annual cycle has to take into account fitness in the other season. If the intrinsic fitness of habitat B in season 2 is sufficiently low, then non-migration may be excluded even in the absence of density dependence (an example of exclusion consistent with this effect is shown in Fig. 3.2). Alternatively, strong negative density dependence from the migrant may sufficiently lower fitness that a non-migrant is excluded—even though a non-migratory population could persist just fine in isolation For example, Fig. 3.1 shows a system where each habitat is initially occupied by a non-migratory species. When migratory morphs are introduced, they rapidly replace one of the specialists.

If survival rates in the non-growing season are identical across habitats ($R_{A2} = R_{B2}$), then there is no fitness advantage between pairs of competing morphs, even if there is pronounced habitat-mediated variation in fitness during the growing season. Habitat A specialists and migrants have equivalent annual fitness, since $R_{A1}{}^* R_{B2} = R_{A1}{}^* R_{A2}$. The same is true of habitat B specialists and perverse migrants, since $R_{B1}{}^* R_{B2} = R_{B1}{}^* R_{A2}$. Constant mortality across habitats leads to all four morphs coexisting in the two habitats, at frequencies dictated by initial conditions (Fig. 3.4), provided that $R_{A1}R_{A2} > 1$ and $R_{B1}R_{B2} > 1$. A very similar process of neutral selection was demonstrated previously in models of habitat-mediated dispersal (McPeek and Holt 1992), where many combinations of dispersal strategies are neutral, relative to each other.

More typically, however, one might expect to see differences in demographic parameters across different habitats. Under these more general conditions, in systems that settle down to demographic equilibrium, at most two out of the four discrete behavioural morphs that we are contrasting can coexist in a system with two habitats, due to direct density-dependent selection between pairs of competing morphs (habitat A specialists vs. logical migrants or habitat B specialists vs. perverse migrants). Only migrants by themselves, or a pair of migratory morphs (logical and perverse migrants), can persist when both habitats are sinks (as assessed by the fate of non-migratory morphs, when alone).

Our general conclusion is that if a species is widely distributed, and the world fluctuates through time (an ecological truism if there ever were one), then if one does NOT observe migration, it must be because migration itself is costly. Such costs are not explicitly built into the logic of fitness in the seasonal environments that we have presented above. However, one can use the general approach sketched above to 'titrate' such costs, so as to determine threshold conditions for when migration would not be favoured because of its intrinsic costs. In particular, assume that there is a multiplicative decrement in fitness of c (for cost) for each bout of migratory movement, expressed as realized seasonal fitness in each habitat. Assume that the highest such fitness is $F_{\text{potential}} \equiv R_{A1}{}^{*}R_{B2}{}^{*} > 1$, so migration should be favoured (the asterisks indicate that there should be density dependence, given that both habitats are occupied, and the population persists without moving between them). If migration is not in fact favoured, that must be because it is costly to move, as measured in a fitness decrement. Incorporating a fitness decrement of c equal in magnitude for each year (habitat A to B, and habitat B back to A), the actual annual fitness is

$$F_{actual} = R^{*}_{A1}R^{*}_{B2} - c. \tag{16}$$

The threshold between migration being favoured and not corresponds to a cost of

$$c = R^{*}_{A1}R^{*}_{B2} - 1. \tag{17}$$

Extending the numerical example discussed earlier, if rare migrants invade a system in which fitness during the growing season is $R_{A1} = 2$ and fitness during the non-growing season in the alternative habitat B is $R_{B2} = 0.7$, then the threshold cost each way required to impede the evolution of migration $c = (2 \times 0.7) - 1 = 0.4$. To illustrate this effect, we apply a travel cost slightly exceeding the threshold for the migratory system modelled in Fig. 3.1. The imposition of a minor energetic cost makes the system vulnerable to re-invasion by the non-migratory specialist in habitat A (Fig. 3.5). Such a cost that (just) prevents migration from being favoured in a temporally variable environment within an occupied geographical range (in our case, two discrete habitats) is determined by the geometric mean of the better seasonal fitnesses across both habitats. The threshold cost per move cannot be assessed just by looking at one habitat, but involves an assessment of fitness benefits across the entire migratory cycle.

So far, we have considered only outcomes in which equilibria are locally stable. It is well known that discrete time models with this structure exhibit population cycles or even deterministic chaos at elevated rates of growth (May 1976). Variation in fitness over time has the potential to influence evolutionary dynamics in any system, including those with spatial structure (McPeek and Holt 1992; Holt and McPeek 1996), so unstable systems are important to consider. Increase in the rate of population growth for our two habitat system typically induces fluctuations in both total population abundance and relative frequencies of each morph (Fig. 3.6). Peaks and troughs in population density are positively correlated with variation in the relative frequency of migrants.

A variation on this expected theme arises when both habitats offer similar growth rates ($r_A = r_B$), but differ in survival rates ($s_B > s_A$). When maximum per capita growth rates are large, migrants and habitat B specialists often show a complex pattern of out-of-phase fluctuation as the migrant behavioural morph invades the ecosystem, but these fluctuations settle down to constant proportions over time, despite the fact that overall population abundance remains highly unstable (Fig. 3.7).

Interestingly, this outcome is sensitive to initial conditions. Slight modifications in the initial

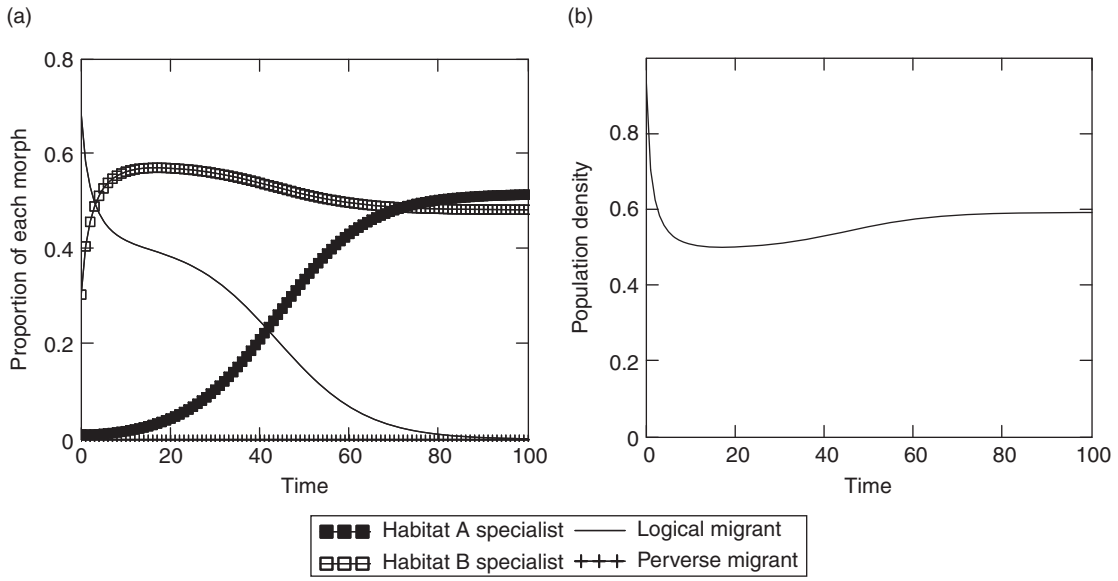

Figure 3.5 Variation over time in the relative frequency of (a) behavioural morphs and (b) population abundance in a system with specialists in two distinct habitats that is invaded by rare morphs that migrate between habitats on a seasonal basis ($r_A = 1.0$, $r_B = 0.5$, $s_A = -0.69$, $s_B = -0.36$). Habitat A is best during the growing season, whereas habitat B is best during the non-growing season. A demographic cost of 0.44 was applied at each habitat transition for migrants. Initial population densities of habitat B specialists and migrants were based on equilibria from the simulation depicted in Fig. 3.1.

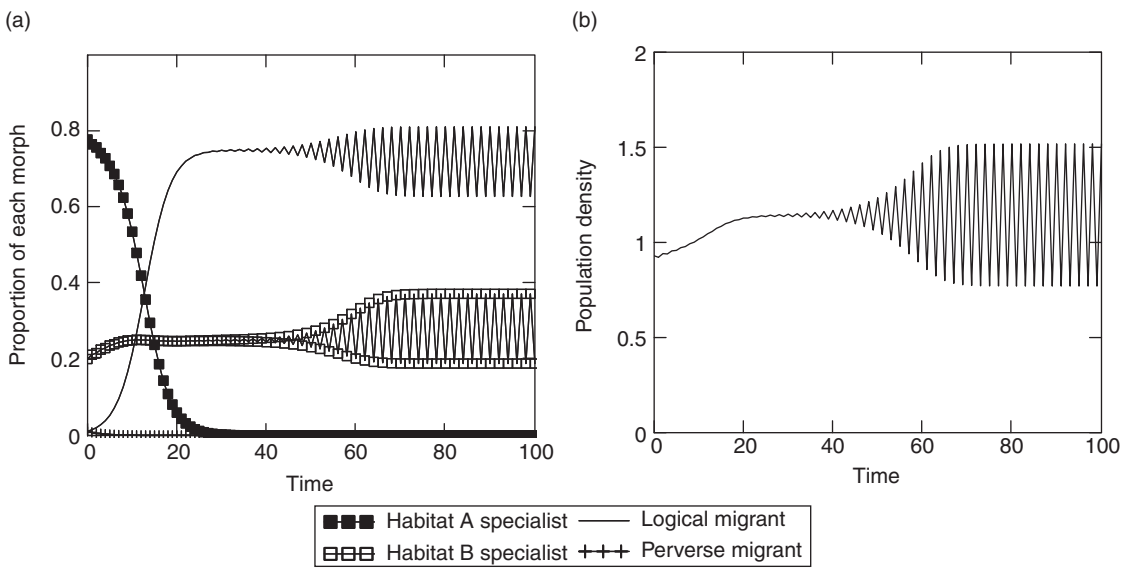

Figure 3.6 Variation over time in the relative frequency of (a) behavioural morphs and (b) population abundance in a system with specialists in two distinct habitats that is invaded by rare morphs that migrate between habitats on a seasonal basis ($r_A = 2.5$, $r_B = 0.5$, $s_A = -0.69$, $s_B = -0.36$). Habitat A is best in the growing season whereas habitat B is best during the non-growing season.

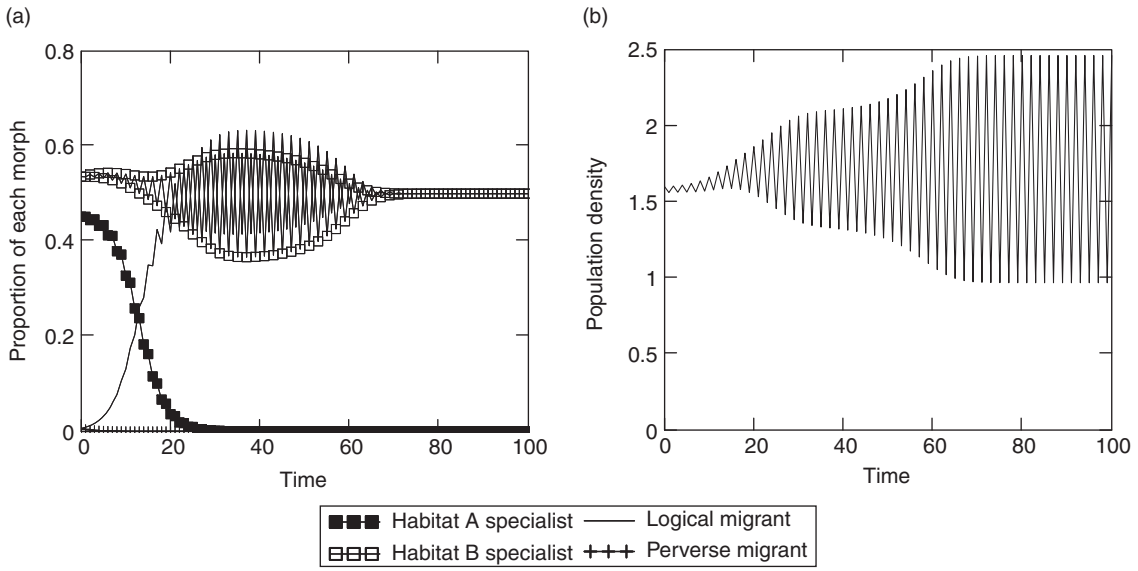

Figure 3.7 Variation over time in the relative frequency of (a) behavioural morphs and (b) population abundance in a system with specialists in two distinct habitats that is invaded by rare morphs that migrate between habitats on a seasonal basis ($r_A = 2.5$, $r_B = 2.5$, $s_A = -0.69$, $s_B = -0.36$). Both habitats are equal during the breeding season whereas habitat B is best during the non-breeding season.

abundance of specialists before the mutant migrant morph invades can produce a mirror-image: population abundance that stabilizes over time, yet with morph frequencies that fluctuate violently over time (Fig. 3.8). In other words, dynamic instability in migratory systems can be expressed through variation in either population abundance or behaviour.

This example suggests that a ripe area for future work will be to examine the interplay of seasonality and intrinsic population instabilities, and how this can both promote migration and potentially lead to counter-intuitive results. Only more detailed analyses, across a range of models, will be able to determine if these intriguing patterns are merely curiosities, or instead arise as surprising outcomes in a broad array of circumstances. The interplay of temporal variation and spatial processes often leads to surprising results, and migration may at times amplify the dynamic complexities inherent in many ecological systems.

3.5 Discussion

Our simple two habitat model captures some of the key biological characteristics that recur in virtually all migratory ecosystems. First and foremost, the evolution of migration requires some interplay between seasonal and spatial variation in fitness (Lack 1968; Fryxell and Sinclair 1988a; Lundberg 1988). Such variation is, of course, nearly ubiquitous in the natural world. One would be hard-pressed not to find spatial variability in critical ecological characteristics across the habitable range of most organisms, particularly those of larger body size. Seasonality, as well, is a hard fact of life, even in the tropics. Alternation between periods of breeding and non-breeding is the norm, rather than the exception, in nature, even if the absence of seasonality is the norm in most ecological theory. Even environments that at first glance seem to be devoid of seasonality (e.g., caves, the deep sea) can be influenced by seasonal variation, if they are coupled to external, variable environments—which they almost always are.

Our model is admittedly—and unashamedly—rather crude. It is useful to summarize these limitations in the model, each of which we suggest represents a potential avenue for further theoretical exploration and refinement of the evolutionary theory of migration.

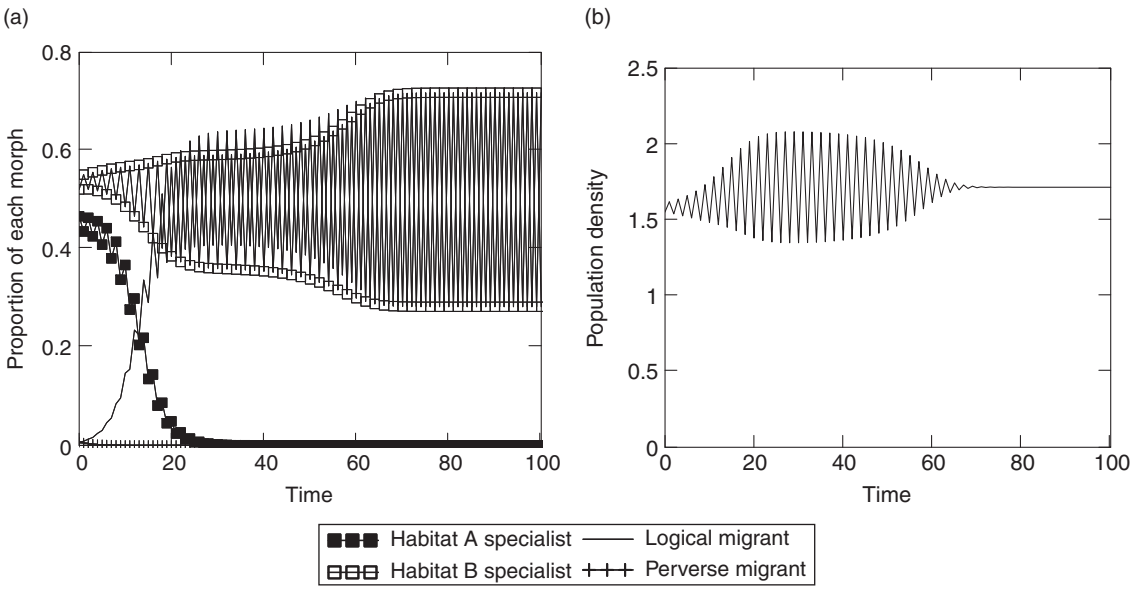

Figure 3.8 Variation over time in the relative frequency of (a) behavioural morphs and (b) population abundance in a system with specialists in two distinct habitats that is invaded by rare morphs that migrate between habitats on a seasonal basis ($r_A = 2.5$, $r_B = 2.5$, $s_A = -0.69$, $s_B = -0.36$). Both habitats are equal during the growing season whereas habitat B is best during the non-growing season. This figure differs from Fig. 3.7 only in a slight difference in initial conditions: In Fig. 3.7, (a) initial population densities set at their equilibria for both habitat specialists; in this figure, habitat specialist A was initiated at equilibrium, whereas habitat specialist B was initiated ~10% below its equilibrium.

We did not account for the ecological and genetic complexities that no doubt occur in real organisms, because we assumed clonal inheritance. Yet most species that migrate are sexual, and migratory behaviour is likely to be under rather complex genetic control (Chapter 2). Even for clonal inheritance, we have not paid attention to the potential for mixed strategies, such as partial migration, say with different propensities to migrate in each habitat. Broadening the range of migratory strategies that are competing with each other, and how they are generated by alternative rules of inheritance, is clearly an important step that would go beyond the models we have presented here. Griswold *et al*. (2010) have developed an excellent template for exploring the intricacies of genetics and demography in migration models of the sort that we have described here.

We have also ignored the crucial role sensory cues can play in the actual mechanisms generating migratory behaviour (Chapter 6). Our simple model presumed in effect that organisms have no ability to anticipate fitness in either their current or alternative habitats and make appropriate decisions. This seems inconsistent with well-documented instances of migratory organisms reversing their migratory circuit under unusual environmental conditions, such as wildebeest returning to the Serengeti plains in years with exceptional dry season rainfall (Maddock 1979).

Space is implicit and admittedly rudimentary in our models. Real migrants must use constrained movement modes to traverse rugged landscapes, with dynamic interplay between navigational capacity, social pressures, and complex motivational goals (Mueller *et al*. 2008; Nathan *et al*. 2008; Schick *et al*. 2008). This in turn makes it likely that some habitats could remain part of a migratory repertoire even if, in terms of the strict calculus of natural selection, such habitats should be ignored.

Our models also, and crucially, do not explicitly include ecological interactions other than direct density-dependent competition between behavioural morphs. Ecological interactions may be implicitly contained, however, depending upon the details. For instance, if one ecological dominant

species migrates, this automatically sets up a seasonal driver in the lives of other, more subordinate species.

Some ecological interactions may need to be specifically modelled, because there are direct feedbacks between the migratory species and these other players in the ecological system (Chapter 9). In our model, there is no explicit resource dependence, predation or disease risk, nor social or agonistic interactions within or among morphs. Incorporating such interactions could permit a more refined assessment about which environments might foster migration, and for which taxa. Moreover, many of these interactions operate with a time lag. Depending on the timing of these lags, they could either magnify, or dampen, the impact of external seasonal drivers on fitness, and thus alter the relationship between seasonality and migration.

Moreover, our model organisms have a simple life history, whereas real organisms can employ state- and age-dependent decisions to maximize lifetime reproductive success, which we know can considerably alter optimal evolutionary strategies (Clark and Mangel 2000, Stephens *et al*. 2007). Even simple models such as ours can employ carryover effects from one season to the next, which can have important population dynamic properties (Ratikainen *et al*. 2007).

Despite all these caveats, a simple model such as the one we have presented is valuable, because it is tractable enough to allow analytical approaches as well as straightforward simulation, a mixture that is often powerful in understanding the full range of possible outcomes of ecological models. In our experience, many insights from simple models such as the ones we have presented provide crucial yardsticks for assessing the importance of the various factors we have listed as potential caveats and complicating factors in the above paragraphs.

There is a substantial published literature on the evolutionary dynamics of dispersal in systems with two or more habitat patches. Limitations on space preclude a detailed review here. Suffice it to say that formal models of invasion dynamics often suggest the coexistence of two or more dispersal morphs in a metapopulation setting (McPeek and Holt 1992; Doebeli 1995; Doebeli and Ruxton 1997; Parvinen 1999). Population dynamics play a key role in maintaining behavioural polymorphism in meta-populations (McPeek and Holt 1992; Doebeli 1995; Doebeli and Ruxton 1997; Parvinen 1999), as does stochastic variation in extinction risk across the ensemble of patches (Heino and Hanski 2001). We have found in our numerical simulations of the seasonal Ricker model that likewise coexistence of alternative migratory morphs can occur. Note that our clonal model can also be interpreted as a model for interactions between two competing species, which are equal with respect to density dependence, when they co-occur. What our model results suggest is that the combination of seasonality and migration can permit species coexistence, despite their competitive equivalence within patches.

It has long been appreciated that geographic variation in survival rates outside the breeding season can contribute importantly to the selective advantage of migration (Lundberg 1988). Lack (1968) pointed out that temporal variation in survival rates could lead to balanced long-term fitness of migrants vs. residents. Similar arguments underlie von Haartman's (1968) state-dependent evolutionary arguments for the evolution of avian migration; resident birds obtain compensatory reproductive advantage balancing the higher over-wintering costs relative to migrants. Both these treatments were well ahead of the development of ESS theory, so it is not surprising that they did not consider conditions for successful invasion by other phenotypes. In a prescient theoretical study, Cohen (1967) developed a formal model of invasion dynamics in the special case of a population with geometric growth with inter-annual variation in λ. Population dynamic effects alone could not create opportunities for invasion by alternate phenotypes, such as those we have shown. As a simplifying assumption, Cohen presumed identical reproductive rates of migrants vs. residents, focusing purely on variation in over-winter survival. Theoretical treatments of migration evolution rarely consider the possibility that residents could exist as an ancestral condition in both habitats.

More recent models on the evolution of migration have typically used more highly structured models and less generic contrasts between habitats (Lundberg 1987; Kaitala *et al*. 1993; Kokko and Lundberg 2001; Griswold *et al*. 2010). For example,

Kaitala *et al*. (1993) evaluate conditions under which over-wintering migration is an ESS in an age-structured population of birds that must breed in one habitat, developing a theme first formally developed by Lundberg (1987) in a graphical model. Over-wintering survival is assumed to be density-independent in migrants, but linearly density-dependent in non-migrant individuals. These conditions are reasonable for many passerine birds, and demographic parameters were chosen accordingly. Kaitala *et al*. (1993) found that mixed strategies (i.e. partial migration) were selected for under conditions of density-dependent over-winter survival. Griswold *et al*. (2010) linked genetic effects with habitat-mediated variation in seasonal fitness, using paired habitats in a similar manner to our model, with an important difference: either reproduction or survival was assumed impossible in one habitat. Griswold *et al*. (2010) found that the evolution of partial migration depended on the genetic basis for behaviour and in which season habitats were shared, demonstrating a clear need for proper linkage of genetic and demographic dynamics in future modelling efforts. Our more generic formulation, with milder seasonality, predicts partial migration as a common outcome except under exceptional conditions of source–sink dynamics. Echoing Kaitala *et al*.'s findings, partial migration requires some form of density dependence, but this can be expressed either for the breeding or non-breeding season.

Where spatial and seasonal variation in fitness does occur, our simple model predicts that migration should often prove selectively advantageous. This assertion may explain why migration has repeatedly evolved in a wide variety of biomes and taxa (Chapter 2). The conditions favouring migration are common, so it is not surprising that this lifestyle has evolved countless times in evolutionary history. Indeed, the conditions favouring migration are so general, it is perhaps more relevant to ask why migration isn't ubiquitous?

One answer to this paradox suggested by our model is that the demographic cost of migration itself may exceed the benefits in some systems. This cost could be expressed in myriad ways. It could be a simple energetic debt that simply cannot be repaid at the end of each arduous journey. Many migrants respond to this challenge through stopover sites en route, used to restore depleted energy reserves (Alerstam *et al*. 2003). Nonetheless, energetic costs may be of sufficient magnitude to compromise individual fitness, particularly for females that must choose wisely between investment of energy reserves in movement vs. production of offspring. In probing this question, it might well prove instructive to compare energetic costs of migration across different taxa and modes of locomotion, particularly in relation to body size (Chapter 4).

The cost of migration could be social, particularly in species where social dominance and therefore access to potential mates depend on acquisition and control of scarce resources, via territoriality or semi-exclusive home range use (Lundberg 1987; Kaitala *et al*. 1993; Kokko and Lundberg 2001). Individuals that reposition each season may lose priority access to favoured patches of real estate, which is untenable in the long-run. For example, territorial lions are seemingly unable or unwilling to track the seasonal migration of large herbivores from the Serengeti plains to the northern woodlands, possibly because of the risk of losing fiercely-defended group territories to neighbouring prides (Mosser *et al*. 2009). It is intriguing to speculate that social costs of migration may be more prevalent in organisms placed at the top of food-webs, where territoriality and complex social dominance are the norm, rather than the exception.

The demographic cost of migration could be expressed through increased exposure to predators, particularly if migrants are easier to find, readily visible, more vulnerable to attack, or less capable of predator avoidance than non-migrants. Grizzly bears congregating along salmon spawning runs or crocodiles lurking at traditional river crossings used by wildebeest instantly leap to mind. There are certainly well-documented examples of humans lying in wait along migratory routes to ambush migratory ungulates, fish or waterfowl (Chapter 11).

Whatever these costs may be, our simple model suggests that they need to be compared with the demographic benefits of migration to realize a full Malthusian accounting. Indeed, our model suggests that it is not enough to think about the ecological characteristics of used habitats—these are only meaningful in comparison with habitats passed up by migrants. Demographic assessment could be

quite challenging, admittedly, if migratory individuals choose not to live in some habitats. One can even imagine experimental titration of the demographic costs vs. benefits of migration allowing rigorous new testing of alternative constraints on the evolution of migration.

Our model suggests that alternate behavioural morphs should be sought as coexisting strategies, as a mixed ESS, in systems with habitat and seasonal structure. The favoured mix of coexisting strategies depends, however, on the magnitude of spatial and temporal variation in vital rates. Systems with seasonal alternation in the habitats with optimal fitness select for migrants that shift seasonally between the best habitats available and non-migrants that specialize in the poorest breeding sites. Systems in which one habitat is always optimal select for habitat specialists in the ideal habitat, mixed with perverse migrants that move away to breed in poor sites before returning to share the non-breeding season with their specialist brethren. Where neither habitat is best during the non-breeding season, anything goes; all combinations of migrants and non-migrants can coexist. We should caution that the particular model we used to illustrate these points assumes that density dependence occurs entirely in one habitat, in one season. Future studies should examine what happens when there is density dependence in both habitats and in both seasons. We surmise that our results will prove to be robust to at least weak density dependence in the second habitat.

It is intriguing that even in our simple model, coexisting migratory strategies are found to robustly persist. Where close study has been conducted, a mixture of migratory strategies often occurs (Lundberg 1988). For example, some elk in the Rocky Mountains migrate seasonally between high and low elevations, yet others in close proximity remain rooted within a small home range year-round (Hebblewhite and Merrill 2007; Hebblewhite *et al*. 2008). Similarly, although most Canada geese migrate between northern latitudes and the southern United States, resident populations also thrive alongside more typical migrants in many northern sites. Such observations are what we might expect, based on the general outcomes of our models. Rarely do we know, however, which pairs of strategies are represented; is a migrant behavioural type exploiting the best of all possible habitat combinations, or is it eking out a second-rate coexistence on poorer breeding habitat? Are non-migrants evolutionary winners or losers, inevitably on their way out, but caught at present in a transient snapshot of temporary coexistence? These alternate possibilities, predicted by our simple model, call for a fresh look at the fitness of migrants vs. residents. We caution again that our specific model assumes that individuals have fixed migratory strategies, and that there are few operative constraints or migratory costs. In some of these empirical examples, individuals may be making the best of a bad situation, for instance, and the evolutionarily stable strategy is in fact a fixed, conditional strategy.

The range of mixed ESS outcomes suggested by our models suggests that it may be more relevant to ask not how migration behaviour has evolved, but rather why we don't always see a mixture of strongly contrasting movement strategies. In our model, a migratory strategy is the only pure ESS provided at least one habitat is a sink, unable to sustain a non-migratory population at all, and the other habitat has sufficiently large temporal variation in fitness or fitness components. Relating this prediction to empirical data will require information both on spatial variation in fitness and temporal variability. This is daunting, but a nettle that must be grasped, if we are ever to understand at a deep level the evolutionary basis of migration.