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To breed or not to breed: a model of partial migration

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ABSTRACT

Migration is used by a number of species as a strategy for dealing with a seasonally variable environment. In many migratory species, only some individuals migrate within a given season (migrants) while the rest remain in the same location (residents), a phenomenon called "partial migration". Most examples of partial migration considered in the literature (both empirically and theoretically) fall into one of two categories: either species where residents and migrants share a breeding ground and winter apart, or species where residents and migrants share an overwintering ground and breed apart. However, a third form of partial migration can occur when non-migrating individuals actually forgo reproduction, essentially a special form of low-frequency reproduction. While this type of partial migration is well documented in many taxa, it is not often included in the partial migration literature, and has not been considered theoretically to date. In this paper we present a model for this partial migration scenario and determine under what conditions an individual should skip a breeding opportunity (resulting in partial migration), and under what conditions individuals should breed every chance they get (resulting in complete migration). In a constant environment, we find that partial migration is expected to occur when the mortality cost of migration is high, and when individuals can greatly increase their fecundity by skipping a year before breeding. In a stochastic environment, we find that an individual should skip migration more frequently with increased risk of a bad year (higher probability and severity), with higher mortality cost of migration, and with lower mortality cost of skipping. We discuss these results in the context of empirical data and existing life history theory.

INTRODUCTION

Migration is used by a number of species, including birds, fish, invertebrates, and mammals, as one strategy for dealing with a seasonally variable environment. In many cases, migration is obligate, but in some species, within a migratory population only some individuals migrate in a given season (migrants), while the rest remain in the same location (residents), a phenomenon called "partial migration" (Dingle 1996).

Partial migration was first described in avian species in which residents and migrants share a breeding ground but overwinter apart (e.g. Lack 1943, 1944). In more recent years, it has been recognized that partial migration can also occur when residents and migrants share a wintering ground but breed in separate locations (e.g. American Dippers; Morrissey et al. 2004). A third form of partial migration occurs when non-migrating individuals actually forgo reproduction – this is essentially a special form of low-frequency reproduction. Figure 1 illustrates these three types of partial migration. Although this third type of partial migration is well documented in salamanders, newts, sea turtles, and many species of fish (see Bull and Shine 1979, Rideout et al. 2005 for reviews), it is not often included in the partial migration literature.

The development of partial migration theory has closely shadowed the empirical studies: the first models of partial migration only considered the case of a shared breeding ground and found that the extent of partial migration should depend on the strength of both density-dependence and environmental stochasticity (Cohen 1967, Lundberg 1987, Kaitala et al. 1993, Taylor and Norris 2007). A more recent

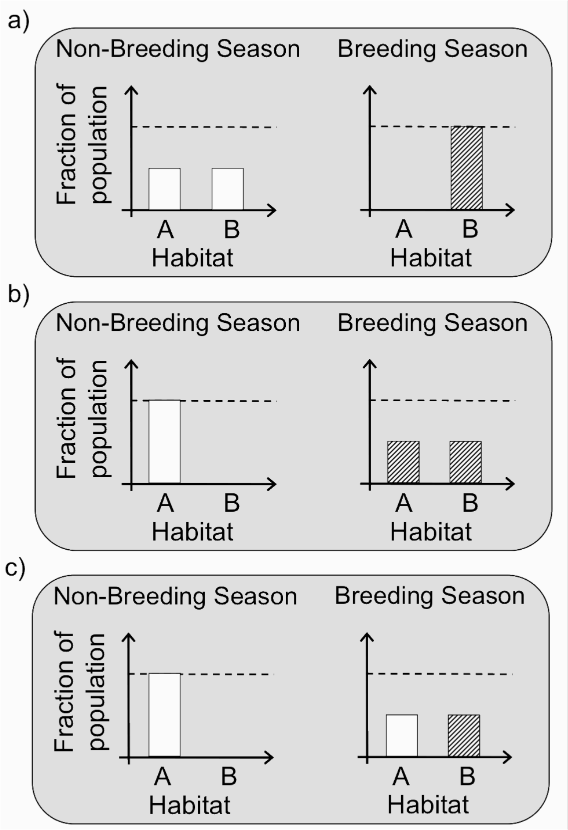

Figure 1. Schematic of three different types of partial migration: a) residents and migrants share a breeding habitat but spend the non-breeding season apart, b) residents and migrants share a non-breeding habitat and breed apart, and c) resident and migrants are apart during the breeding season, but since migration is required for reproduction only migrant individuals reproduce. Each panel shows the fraction of the population in each of the two habitats (A and B) during each of two seasons (non-breeding and breeding). Shaded bars indicate individuals that are reproducing.

theoretical paper found that that the scenarios of shared-breeding and shared-wintering migration are not equivalent and can lead to different amounts of partial migration (Griswold et al. 2010). However, no models have yet considered the third type of partial migration, where individuals that do not migrate skip reproduction altogether. Unlike the first two types of partial migration, which involve mainly tradeoffs in space (e.g. between one location with low survival and another with high competition), the third type involves a tradeoff in time (between current and future reproduction). As such, it seems likely that current theory would not apply to this type.

Our goal is to understand what conditions lead to partial migration in this third scenario. In this paper we present a model of the evolution of partial migration in species where, in a given season, individuals either migrate and reproduce, or skip migration and forgo reproduction. We determine under what conditions individuals should breed at every opportunity, and under what conditions they should skip some breeding opportunities. We also examine the effect of environmental stochasticity on optimal migratory behavior.

LOW-FREQUENCY BREEDING MIGRATIONS

In this paper we consider partial migration in species with low-frequency breeding migrations. For example, most baleen whales feed at high latitudes, and migrate to low latitude breeding grounds to reproduce (Corkeron and Connor 1999). Adult land crabs are terrestrial but their eggs must develop in seawater and so adult females migrate to the coast to release their eggs in the sea (Wolcott 1988). Similarly, many adult amphibians that live terrestrially need to migrate back to ephemeral ponds to reproduce (Russell et al. 2005). Adult sea turtles spend most of their lives foraging at sea but migrate back to specific beaches in the tropics to nest (Musick and Limpus 1997). In each of these cases, an individual spends the majority of its life in one habitat, but must make a costly migration to another location in order to reproduce. In most years, a fraction of the population will actually skip migration and forgo reproduction (Table 1).

Breeding migrations often have a high mortality cost, such that the annual survival of an individual that chooses to migrate and reproduce (σ_r) is often much lower than that of an individual that chooses to skip migration and reproduction (σ_s). For our purposes, we assume that $\sigma_r = (1\text{-}m)\sigma_s$ where m is a measure of the relative mortality cost of migration ($0 \leq m \leq 1$).

While migrating individuals have a lower survival, they gain the benefit of immediate reproduction (with fecundity φ), whereas individuals that skip migration must wait until a future opportunity to reproduce. In many species with breeding migration (such as sea turtles, salmon and land crabs), individuals store energy across seasons and only migrate when they reach a certain threshold (Thorpe 1994, Hays 2000, Solow et al. 2002, Caut et al. 2008, Hartnoll pers. comm.). Therefore it seems reasonable to assume that fecundity is higher for a reproducing individual that skipped the breeding opportunity the previous year (φ_2), than for a reproducing individual that did not skip reproduction the previous year (φ_1).

The question is, given these tradeoffs, under what conditions does it pay for an individual to skip a breeding opportunity? Suppose an individual reproduces in a given year, after having reproduced the previous year, with probability θ. Alternatively, it skips a breeding opportunity with probability $1\text{-}\theta$. The best strategy, if it exists, is the Evolutionarily Stable Strategy (ESS), which we denote θ^* – the value of θ that, when adopted by a population of individuals, cannot be invaded by a mutant with any other value of θ (Maynard Smith and Price 1973). A value of θ^* less than one indicates that the best individual strategy

Table 1. Known examples of species with breeding migrations where at least some individuals skip migration each year. Species names (latin and common), the frequency of breeding when known, and the reference for each is given.

Species	Frequency	Reference
Crustaceans		
Callinectes sapidus (blue crab)	some skip	Aguilar et al. 2005
Gecarcinus ruricola (black land crab)	some skip	Hartnoll et al. 2007
Gecarcoidea natalis (Christmas Island red crab)	some skip	Green 1997
Fish		
Galeorhinus australis (Australian school shark)	2 yrs	Olsen 1954
Acipenser fulvescens (Lake sturgeon)	4-6 yrs	Scott and Crossmann 1973
Acipenser transmontanus (White sturgeon)	4-11 yrs	Scott and Crossmann 1973
Clupea harengus (Atlantic herring)	1-2 yrs	Engelhard and Heino 2005
Catostomus commersonii (White sucker)	some skip	Quinn and Ross 1985
Salmo salar (Atlantic salmon)	1-2 yrs	Jonsson et al. 1991
Salvelinus malma (Dolly varden)	1-2+ yrs	Scott and Crossmann 1973
Hoplostethus atlanticus (Orange roughy)	some skip	Bell et al. 1992
Lates calcarifer (Barramundi)	some skip	Moore and Reynolds 1982
Acanthopagrus australis (Surf bream)	some skip	Pollock 1984
Amphibians		
Ambystoma maculatum (spotted salamander)	1-4yrs	Husting 1965
Taricha granulosa (rough-skinned newt)	1-2 yrs	Pimentel 1960
Taricha rivularis (red-bellied newt)	2-3 yrs	Twitty et al. 1964
Taricha torosa (California newt)	2 yrs	Bull and Shine 1979
Triturus alpestris (Alpine newt)	1-2 yrs	Bull and Shine 1979
Mammals		
Megaptera novaeangliae (humpback whale)	some skip	Craig and Herman 1997
Physeter macrocephalus (sperm whale)	some skip	Mellinger et al. 2004
Reptiles		
Iguana iguana (green iguana)	1-2 yrs	Bock et al. 1985
Caretta caretta (loggerhead sea turtle)	1-6 yrs	Hatase et al. 2002
Chelonia mydas (green sea turtle)	2-4 yrs	Mortimer and Carr 1987
Dermochelys coriacea (leatherback sea turtle)	2-7 yrs	Saba et al. 2007
Eretmochelys imbricata (hawksbill sea turtle)	3-6 yrs	Carr and Stancyk 1975
Lepidochelys kempii (Kemp's ridley sea turtle)	1-4 yrs	Pritchard and Márquez 1973
Lepidochelys olivacea (olive ridley sea turtle)	1-4 yrs	Schulz 1975
Natator depressus (flatback sea turtle)	2-4 yrs	Hughes 1995

is to skip some breeding opportunities, which results in a partially migratory species. Alternatively if θ^* is one, this indicates that the best strategy for an individual is to reproduce annually, which results in a completely migratory population.

The simplest model is where an individual either reproduces annually or skips exactly one year before reproducing. Based on the above assumptions, our model is given by

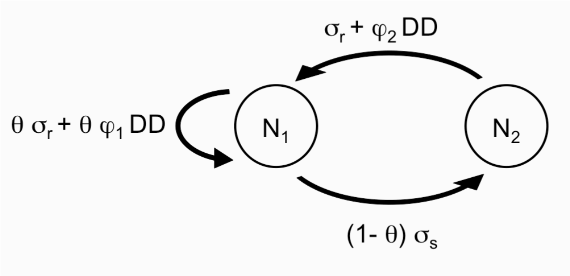

Figure 2. Life cycle graph of our two-stage matrix model (1) where N_i is the number of individuals who have gone i years since last reproducing, φ_i is their corresponding fecundity, σ_r and σ_s are the annual survival rates of individuals that reproduce and skip reproduction respectively, θ is the probability than an individual reproduces annually, and DD is the density-dependence term (2).

$$N(t+1) = \begin{bmatrix} \theta\sigma_r + \theta\varphi_1 DD & \sigma_r + \varphi_2 DD \\ (1-\theta)\sigma_s & 0 \end{bmatrix} N(t) \tag{1}$$

where $N(t) = [N_1(t), N_2(t)]$, N_1 are individuals that reproduced during the previous season and N_2 are individuals that skipped reproduction during the previous season. This is a discrete-time matrix population model, where time (t) corresponds to sequential potential breeding opportunities (e.g. years) and each class (N_i) corresponds to an individual's 'condition,' the number of seasons since it last reproduced. The fecundity of an individual in each of these two classes is given by φ_1 and φ_2 respectively, where $\varphi_1 \leq \varphi_2$, and these values include density-independent mortality. The density-dependence is assumed to be continuously differentiable, and otherwise (DD) can be of any form as long as

$$DD(N_1 = 0, N_2 = 0) = 1 \ , \tag{2a}$$

$$\frac{\partial DD}{\partial N_1} < 0 \ , \tag{2b}$$

$$\text{and } \frac{\partial DD}{\partial N_2} < 0 \, . \tag{2c}$$

This can be viewed as representing either competition among adults (adults compete for a limited number of breeding sites and only those that are successful can reproduce) or as competition among eggs (all reproducing adults produce eggs, only a fraction of which survive).

Individuals that skip a breeding opportunity move up a condition class. All individuals that have reproduced move back into the N_1 class, having exhausted their energy stores, and all new individuals start in this class (see Figure 2). For species with a juvenile phase, where individuals go through one or more seasons before they become sexually mature, the juvenile survival rate is also included in the φ_i DD term.

Under our model, a population is only viable (does not decay to zero) if the condition

$$1-\left[\theta\sigma_r+(1-\theta)\sigma_s\sigma_r\right]<\theta\varphi_1+(1-\theta)\sigma_s\varphi_2 \tag{3}$$

is met. If (3) holds, then the stable equilibrium is given by

$$\overline{N}_1(\theta)=\frac{1}{\beta K(\theta)}\ln\left[\frac{\theta\varphi_1+(1-\theta)\sigma_s\varphi_2}{1-\sigma_r\left[\theta+(1-\theta)\sigma_s\right]}\right] \tag{4a}$$

$$\text{and } \overline{N}_2(\theta)=\frac{(1-\theta)\sigma_s}{\beta K(\theta)}\ln\left[\frac{\theta\varphi_1+(1-\theta)\sigma_s\varphi_2}{1-\sigma_r\left[\theta+(1-\theta)\sigma_s\right]}\right] \quad . \tag{4b}$$

If the fecundity rates φ_1 and φ_2 are too high, this fixed-point equilibrium will become unstable and the system goes through a series of bifurcations leading to stable periodic, quasi-periodic, and chaotic attractors, in turn. Since most biological systems have relatively low fecundity rates (see Fig.2 in Hassell et al. 1976), for the purpose of this paper we only consider the region of parameter space with a stable fixed-point equilibrium, and leave the rest of parameter space for discussion in a future paper.

TO SKIP OR NOT?

To determine under what conditions an individual should skip a breeding opportunity, we can calculate θ* (the ESS value of θ) analytically (see Appendix) as

$$\theta^* = 1 \qquad \text{if} \qquad \frac{\varphi_1}{1-\sigma_r} > \frac{\sigma_s\varphi_2}{1-\sigma_s\sigma_r} \tag{5a}$$

$$\theta^* = 0 \qquad \text{if} \qquad \frac{\varphi_1}{1-\sigma_r} < \frac{\sigma_s\varphi_2}{1-\sigma_s\sigma_r} \ . \tag{5b}$$

This is to say that θ* = 1 (all adults reproduce every season; complete migration) if the ratio of growth to death rate for individuals reproducing immediately exceeds the same ratio for individuals skipping one year and then reproducing, and that θ* = 0 (adults skip every other breeding season; partial migration) if the reverse is true. Note that the value of θ* is never intermediate between zero and one, which is quite unusual for a model containing density-dependence.

From these results we expect that partial migration should occur in cases where the mortality cost of migration is high ($\sigma_r << \sigma_s$) and in cases where fecundity can be greatly increased by skipping a year before breeding ($\varphi_1 << \varphi_2$). There is evidence from biological systems to support both of these conditions. Atlantic salmon (*Salmo salar*) have anadromous migrations where they spend most of their lives in the ocean but migrate into rivers to spawn. Individuals that spawn in smaller rivers have higher post-spawning survival (lower migration mortality cost) and tend to reproduce annually whereas individuals that spawn in larger rivers have lower post-spawning survival (higher migration mortality cost) and breed biennially (Jonsson et al. 1991). For all species of sea turtles, individuals spend most of their lives foraging in the open ocean, but migrate back to their natal beaches when they reproduce. Differences in remigration interval (number of years between breeding) seems to be mainly related to foraging rates of adults; in both loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles, individuals that forage in more nutrient rich areas (faster energy accumulation; higher φ_1) have shorter remigration intervals that those that forage in more nutrient poor areas (Hatase et al. 2004, Caut et al. 2008). Jørgensen et al. (2006) developed a model of partial migration specifically for the Northeast Arctic stock of Atlantic cod (*Gadus morhua*), which migrates from feeding grounds in the Barents sea to spawning grounds off Lofoten. Under their model they predict that the frequency of skipping should increase when the cost of migration is higher, which also matches our model results.

STOCHASTICITY & BET-HEDGING

Many species with breeding migrations face variable environmental conditions, e.g. variation in fecundity. In the Christmas Island red crab (*Gecarcoidea natalis*), a species of land crab, adults are fully terrestrial but their eggs must develop in sea water. This leads to mass migrations by adults to breed and spawn their eggs into the ocean each year. Juvenile crabs spend a few weeks in the ocean before returning to land, but there is high variation in inter-annual juvenile survival; in some years juveniles cover the beaches as they return from the sea and in other years there are so few that they escape detection (Gibson-Hill 1947). Similarly, sea turtles face inter-annual variation in sea surface temperature, which affects upwelling of nutrient-rich water, and in turn likely leads to inter-annual variation in fecundity (Solow et al. 2002, Saba et al. 2007).

We included environmental stochasticity in our model to determine how it would affect optimal migratory behavior. We implemented stochasticity by allowing fecundity to vary randomly across years. We assumed that at each time t the environment was randomly in one of two possible states, A and B, with probability p and 1-p respectively. State A represents a 'bad' year where $\varphi_1 = \varphi_{1lo}$ and $\varphi_2 = \varphi_{2lo}$ (with $\varphi_{1lo} \leq \varphi_{2lo}$), and state B represents a 'good' year where $\varphi_1 = \varphi_{1hi}$ and $\varphi_2 = \varphi_{2hi}$ (with $\varphi_{1hi} \leq \varphi_{2hi}$), with the assumption that all classes have equal or higher fecundity in good years than bad ($\varphi_{1lo} \leq \varphi_{1hi}$ and $\varphi_{2lo} \leq \varphi_{2hi}$). With stochastic fluctuations, the population size is no longer constant and the value of θ* must be calculated in terms of the average growth rate, where the average is taken across all the population sizes that the system visits (see Appendix). Since the distribution of population sizes cannot be expressed analytically, it must be simulated. For simulations we used Ricker-type density-dependence of the form

$$DD = e^{-\beta[\theta\varphi_1 N_1(t)+\varphi_2 N_2(t)]} \tag{6}$$

where β is a constant (Ricker 1975). Using a different form of density-dependence did not qualitatively change our results.

As in the deterministic model, the value of θ* was often zero or one. However there were cases where an intermediate value of θ* evolved, suggesting an additional mechanism that can select for postponing reproduction and partial migration. An intermediate value of θ* means that there is a mixture of strategies within the population, with some individuals reproducing annually and some biennially (or, equivalently, individuals changing between annual and biennial strategies within their lifetime). Intermediate values of θ* evolved under environmental conditions where some years favored θ = 0 strategies and some years favored θ = 1 strategies. This only occurred in regions of parameter space that are close to the boundary defined by condition (5). For example, consider a scenario where good years favor reproducing annually and bad years favor skipping reproduction. The higher the risk of a bad year (higher probability of a bad year, lower fecundity in a bad year), the lower the value of θ* (Figure 3). Additionally, the lower the cost to postponing reproduction (smaller difference between the fitness of θ* = 0 and θ = 1 strategies), the higher the level of bet-hedging selected for (Figure 4a). Finally, the more costly migration is (higher m), the more often individuals will skip reproduction (Figure 4b).

From these results we expect that intermediate values of θ* should occur in populations where environmental variation results in conditions that fluctuate between favoring annual reproduction and postponing reproduction. Testing this in biological systems requires long-term monitoring of individuals within multiple populations, and being able to quantify environmental variability in each population. Not surprisingly, such studies are rare. However, there is evidence from sea turtles that suggests that variation in remigration intervals of both green (*Chelonia mydas*) and leatherback sea turtles is related to temporal variation in sea surface temperature (Solow et al. 2002, Saba et al. 2007). Additionally, a recent study compared life-history strategies of two populations of Black-browed albatross (*Thalassarche melanophrys*), one breeding at South Georgia in the Atlantic Ocean and the other breed at Kerguelen in the Indian Ocean. The authors found that albatrosses in the first, more variable population, skipped breeding more often than individuals in the second population (Nevoux et al. 2010). Albatrosses that skip breeding do not actually skip migration, so this example does not quite fit the scenario for our model.

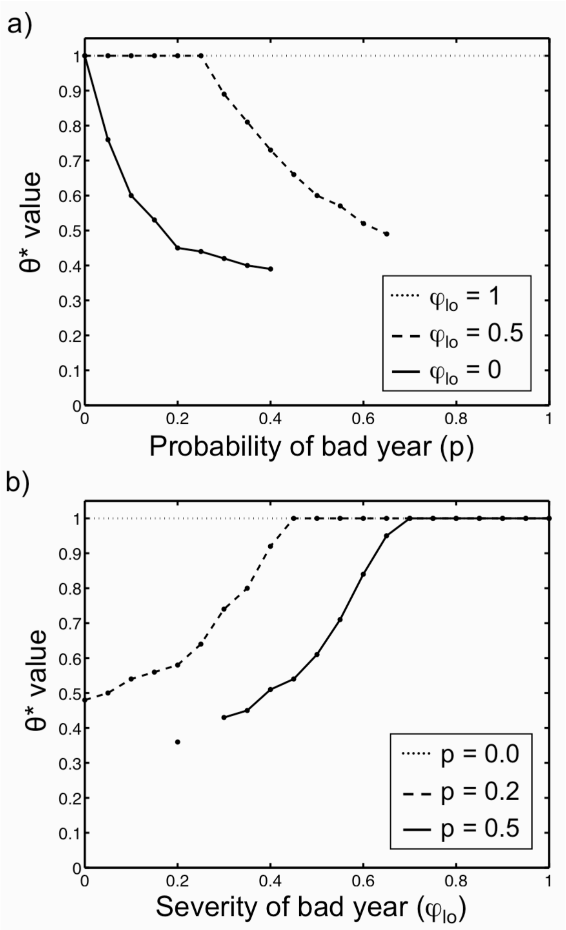

Figure 3. The ESS value of θ (θ^*) as a function of (a) p, the probability of a bad year occurring, and (b) φ_{lo}, the fecundity of both classes in a bad year (the severity of a bad year). Dotted lines show values of θ^* in simulations with no stochasticity, and dashed and solid lines show values of θ^* in simulations with different amounts of stochasticity. For parameter combinations where the population was not viable, the ESS could not be calculated and therefore was not plotted. All simulations were run with $\varphi_{1hi} = \varphi_{2hi} = 3$, $\sigma_s = 0.9$ and $m = 0.9$.

However, this is one of the only examples with sufficient data that details how organisms adjust their breeding behavior in response to environmental stochasticity.

DISCUSSION

Partial migration, in which only some individuals in a population migrate while the rest do not, is common across a variety of taxa. The majority of partial migration studies, both empirical and theoretical, focus on species where both migrants and non-migrants reproduce annually and either share breeding or share wintering grounds. However, in a subset of species with partial migration only the migrants reproduce, and non-migrants by skipping migration forgo reproduction. Existing partial

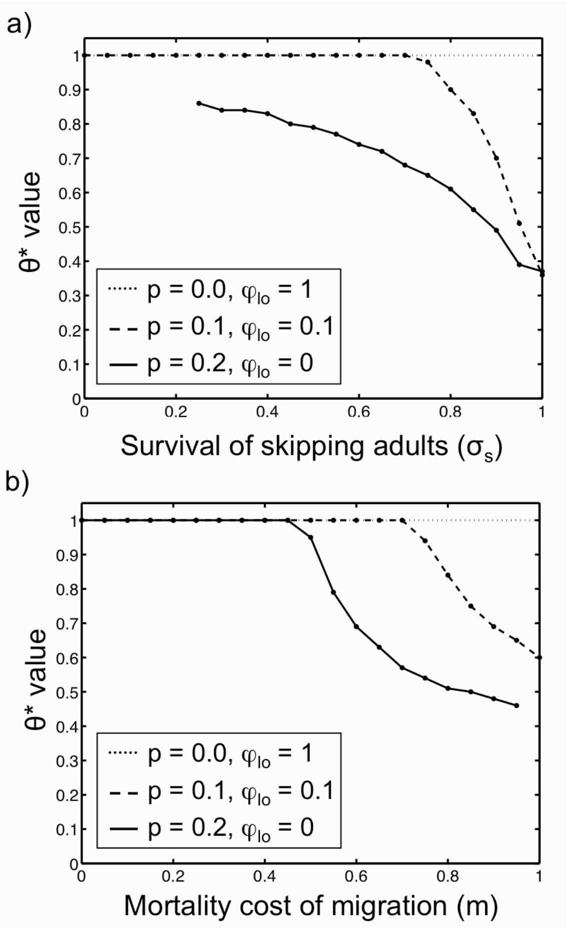

Figure 4. The ESS value of θ (θ^*) as a function of (a) σ_s, the annual survival probability of an individual postponing reproduction; and (b) m, the relative mortality cost of reproducing. Dotted lines show values of θ^* in simulations with no stochasticity, and dashed and solid lines show values of θ^* in simulations with different amounts of stochasticity. For parameter combinations where the population was not viable, the ESS could not be calculated and therefore was not plotted. All simulations were run with $\varphi_{1hi} = \varphi_{2hi} = 3$, $\sigma_s = 0.9$ and $m = 0.9$ unless otherwise indicated.

migration models, which focus on tradeoffs between survival and competition, cannot be applied to these species where behavior is driven instead by a tradeoff between current and future reproduction.

In this paper we present a model for this partial migration scenario and determine under what conditions an individual should skip a breeding opportunity, and under what conditions individuals should breed every chance they get. Our model is simplistic in that it only allows the possibility of skipping a single year, not two or more (which many species are known to do). The main goal of our model was to understand general trends in skipped breeding migrations. Extending the model to allow for extensive skipping would be analytically much more difficult and would, we believe, still produce generally similar trends.

We looked at the extent of partial migration in both constant and stochastic environments. In a constant environment, we find that partial migration is expected to occur when the mortality cost of migration is high, and when individuals can greatly increase their fecundity by skipping a year before breeding. Both of these predictions are supported in the empirical literature (in leatherback and loggerhead sea turtles, and Atlantic salmon, discussed above). In a stochastic environment, we find that an individual should skip migration more frequently with increased risk of a bad year (higher probability and severity). We also find that individuals should be more likely to skip migration when the mortality cost of migration is high, and when the mortality cost of skipping is low. While our specific results are not directly comparable to those of models of the other two types of partial migration (where both residents and migrants reproduce annually and share either a wintering or breeding ground), our results with respect to environmental stochasticity are generally similar: we find that it is possible to explain partial migration without invoking environmental stochasticity (as in Kaitala et al. 1993), but that environmental stochasticity, when included, influences the degree of partial migration (as in Cohen 1967).

Our model could potentially be used to understand the evolution of skipped breeding (also termed “intermittent breeding”) in general. Skipped breeding has been observed in a number of species that have a high ‘accessory’ cost associated with reproduction, of which migration is just one example (Bull and Shine 1979). In these cases, it is thought that adults tradeoff current reproductive success in favor of future reproduction (the prudent parent hypothesis; Le Bohec et al. 2007), as in the case of our model. Skipped reproduction is also observed in species with annual breeding opportunities where the total reproductive cycle is longer than 12 months (e.g. blue king crabs; Jensen and Armstrong 1989), which can be trivially accounted for in our model by setting to φ_1 zero (individuals that try to reproduce again mid-cycle produce no offspring). A third reason some species skip breeding is when breeding must be alternated with another, usually maintenance, activity where both cannot be completed within 12 months, such as moult in birds (Langston and Rohwer 1996). This scenario is not as easily accounted for by our model, but it has been found in state-dependent life history models (e.g. Barta et al. 2006).

Our results, while novel in the field of animal migration are similar to existing results in other areas of life-history theory. For example, in a model of age at first reproduction, Gårdmark et al. (2003) found that organisms should first reproduce as two-year-olds instead of three-year-olds when

$$f_2 > \frac{cf_3 s_2}{1 - s_3} \qquad (7)$$

where f_i is the fecundity at age i, s_i is the survival probability at age i, and c is the added cost of early reproduction, or in other words, when the fecundity of two-year-olds, discounted by the cost of early reproduction and probability of surviving as a two-year-old, is greater than the fecundity of three-year-olds, discounted by the probability of dying between two and three years of age. This finding, which is quite similar to our equation (5), suggests that similar pressures determine age at first reproduction and breeding frequency.

There are also parallels from past theoretical studies on dormancy. Cohen (1966, 1968) developed a density-independent model of optimal reproduction in an annual plant to determine what fraction of seeds should germinate immediately, and what fraction should go dormant before germinating at a later date, given some environmental uncertainty. These models predict that the fraction of seeds germinating should decrease with both increased probability of a bad year and with increased viability of dormant seeds. These results, which closely parallel our own (Figure 3a, 4a), suggest that skipping breeding is essentially a form of reproductive dormancy. Ellner (1985a, 1985b) showed that adding density-dependence to the Cohen model reversed some results: germination can increase with increased probability of a bad year (if the probability is between 0.5 and 1). We did not find evidence in support of this, although for our simulations the population was never viable at such high probabilities of a bad year (Figure 3a). Roerdink (1987) and Tuljapurkar and Istock (1993) each present stage-structured version of the Cohen model (with equal fecundity in all classes) and found that, with environmental stochasticity, the best strategy is to have an intermediate fraction of seeds diapausing (better than none or all). This does not match our finding that there are cases under which the best strategy is to have no individuals skipping migration (equivalent to no diapause). Menu et al. (2000) present a stochastic simulation model for extended diapause in chestnut weevil larvae, where a fraction of individuals have one year of diapause and the rest have two years of diapause. They find that when survival during the extra diapause year is low, the optimal strategy is only to diapause for a single year. On the other hand, when survival during diapause is high, the optimal strategy is to have some larvae diapause one year and some two years. Survival during diapause in this case is analogous to survival when skipping reproduction in our model, and these results match ours (Figure 4b).

In the non-stochastic version of our model, very large values of φ_1 and φ_2 lead to equilibrium population sizes that are periodic or chaotic, not a fixed point. Although we leave extensive exploration of this behavior for a future paper, we found that fluctuations in population size acted like environmental stochasticity in that they selected for ESS values of θ intermediate between 0 and 1. It has previously been demonstrated that fluctuations in population size alone are enough to select for dormancy behavior (Ellner 1987, Lalonde and Roitberg 2006).

Our model provides the first theoretical framework for partial migration in species where individuals that do not migrate actually forgo reproduction. We predict conditions under which partial migration should occur, in both constant and stochastic environments. Our model is useful for understanding the general conditions affecting the degree of partial migration in a species. It could be further tested by comparing data on the actual fraction of a population that skips migration with estimates generated by the model. However to do so would require parameterizing the model with biological data that is not easy to obtain: annual survival of both migrating and non-migrating individuals, and estimates of average fecundity as a function of the years since an individual last reproduced.

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APPENDIX

To determine under what conditions an individual should skip a breeding opportunity, we calculate θ* (the ESS value of θ) as follows.

Without stochasticity, the population size is constant and θ* can be found analytically (Metz et al. 1992, Ferriere et al. 1995, Caswell 2001, McGill and Brown 2007). The growth rate of a mutant type (with $\theta = \theta_M$) in a resident population (with $\theta = \theta_R$) is given by

$$G(\theta_M, \theta_R) = \max(\lambda_J) \tag{A1}$$

where λ_J are the eigenvalues of the Jacobian, **J**, for a mutant in a resident population given by

$$J[\overline{N}(\theta_R)] = \begin{bmatrix} \theta_M \sigma_r + \theta_M \varphi_1 e^{-\beta[\theta_R \varphi_1 \overline{N}_1(\theta_R) + \varphi_2 \overline{N}_2(\theta_R)]} & \sigma_r + \varphi_2 e^{-\beta[\theta_R \varphi_1 \overline{N}_1(\theta_R) + \varphi_2 \overline{N}_2(\theta_R)]} \\ (1 - \theta_M)\sigma_s & 0 \end{bmatrix} \tag{A2}$$

where $\overline{N}(\theta_R) = [\overline{N}_1(\theta_R); \overline{N}_2(\theta_R)]$ is the resident population size at equilibrium, given by equation (4). The ESS is the value θ* such that

$$G(\theta^*, \theta^*) > G(\theta_M, \theta^*)$$

or

$$G(\theta^*, \theta^*) = G(\theta_M, \theta^*) \text{ and } G(\theta^*, \theta_M) > G(\theta_M, \theta_M) \tag{A3}$$

for all values of θ_M. If θ* = 1, then all sexually mature adults reproduce every season. Any value of θ* < 1 indicates partial migration, where at least a fraction of the population forgoes reproduction and migration in a given season.

With stochasticity, the population size is no longer constant and the value of θ* must be calculated in terms of the average growth rate, where the average is taken across all the population sizes that the system visits (Metz et al. 1992, Ferriere et al. 1995, Caswell 2001, McGill and Brown 2007). The average growth rate of a mutant type (with $\theta = \theta_M$) in a resident population (with $\theta = \theta_R$) is given by

$$G_{avg}(\theta_M, \theta_R) = \left| G(\theta_M, \theta_R) \right|^{1/T} \tag{A4}$$

where

$$G(\theta_M, \theta_R) = \max(\lambda_{J'}) \qquad \text{(A5)}$$

and $\lambda_{J'}$ are the eigenvalues of the composite Jacobian, **J'**, for a mutant in a resident population given by

$$J' = J\left[N(\theta_R, 1)\right] * J\left[N(\theta_R, 2)\right] * \ldots * J\left[N(\theta_R, T)\right] \ . \qquad \text{(A6)}$$

Here, $J\left[N(\theta_R, t)\right]$ is the Jacobian for a mutant in a resident of population size $N(\theta_R, t)$ given by equation (A2) and T is the number of points in the resident population's attractor (if the attractor is chaotic or stochastic, take $T \rightarrow \infty$), and $N(\theta_R,1)$, $N(\theta_R,2)$,…, $N(\theta_R,T)$ are the resident population sizes at each attractor point. The ESS is the value θ^* such that

$$G_{avg}(\theta^*, \theta^*) > G_{avg}(\theta_M, \theta^*)$$

or

$$G_{avg}(\theta^*, \theta^*) = G_{avg}(\theta_M, \theta^*) \text{ and } G_{avg}(\theta^*, \theta_M) > G_{avg}(\theta_M, \theta_M) \qquad \text{(A7)}$$

for all values of θ_M. This method produces the same results as equation (A3) above if the resident goes to a fixed-point ($T=1$).

If the distribution of population sizes can be described in closed form, the entire calculation could be done analytically. Benaïm and Schreiber (2009, section 5.1) analyze an unstructured model with density-dependence in a correlated environment, but are only able to get a closed form description of the distribution of population sizes when the correlation is close to perfect. In our case, the environment (as defined by both the random fecundity values, which are not correlated, and resident population size, which is correlated) is only partially correlated, therefore a closed form solution is likely impossible. However, it may be possible to derive an analytic expression for the viability of a population in a stochastic environment – essentially a stochastic version of equation (3) – by assuming a different form of stochasticity (gamma-distributed noise) and following the methodology of Roerdink (1987) and Benaïm and Schreiber (2009).

Since we could not describe the distribution of resident population in closed form in the stochastic version of our model, we had to find the ESS value of θ via iterative simulations as follows. First we picked a value of θ as θ_R and simulated the resident population for 100 steps from a random initial condition. We then simulated the resident population for 10,000 more steps to generate a distribution of resident population sizes, $N(\theta_R,1)$, $N(\theta_R,2)$,…, $N(\theta_R,T)$. If the resident population was not viable (decayed to a population size less than one), the process was started over with a different value of θ_R. If the resident population was viable, we then calculated the growth rate of several different mutant types (with θ_M values near θ_R) analytically, according to equations (A4-6). If any mutant had a higher growth rate than the resident type, then the mutant type with the highest average growth rate according to (A4) was saved as the new resident type (new value for θ_R). The process was repeated from the beginning until a resident type, θ^*, was found that resisted invasion by a mutant (grew faster than all mutant types) for 5 sequential iterations. This was considered to be the ESS value of θ.

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Erratum

Shaw, A. K., and Levin, S. A. To breed or not to breed: a model of partial migration. – Oikos 120: 1871 – 1879.

Equation 4 should read

$$\overline{DD} = \frac{1 - \sigma_r \left[\theta + (1-\theta)\sigma_s \right]}{\theta\phi_1 + (1-\theta)\sigma_s\phi_2}. \tag{4}$$

This is the correct equilibrium condition, given that we have not specified a form of density-dependence at this point in the paper. Once we assume a specific form of density-dependence (e.g. Ricker type as given by Eq. 6), then we can solve for the values of $\overline{N}_1$ and $\overline{N}_2$ explicitly. Equation 4 as shown in the original paper is the equilibrium assuming Ricker density-dependence.

Note that this correction does not affect any of our results.