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Theoretical Ecology

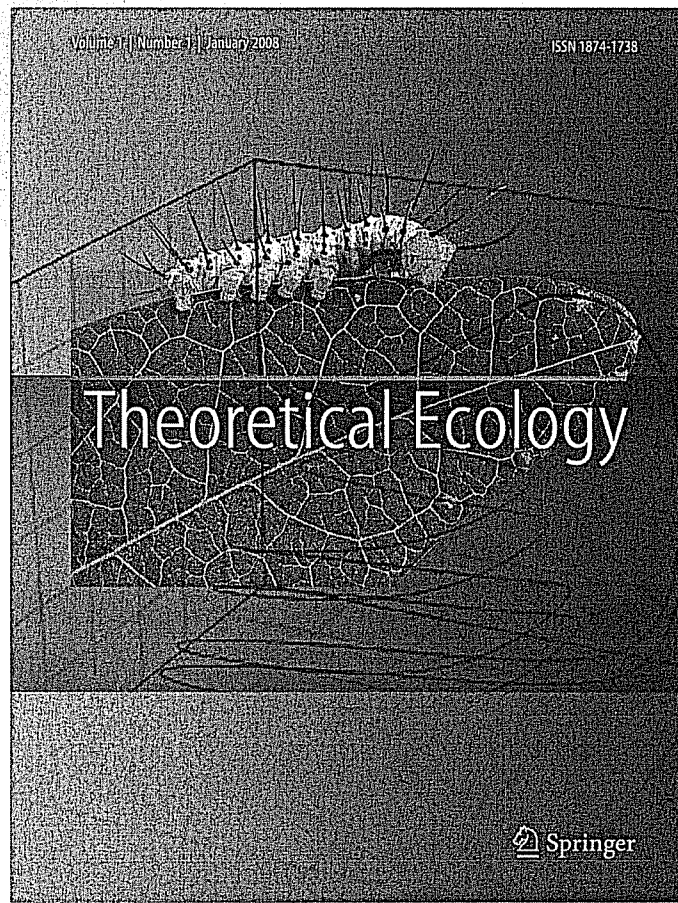
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Leadership, social learning, and the maintenance (or collapse) of migratory populations

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Abstract Long-distance animal migrations are complex, population-level phenomena that emerge in seasonal landscapes as a result of the interplay between environmental influences (e.g., resources, predators) and social interactions among conspecifics. When landscapes change with respect to phenology or connectivity, the dynamics of migratory species can abruptly shift, in many cases leading to a cessation of migration and dramatic decreases in population size. We develop a difference equation modeling framework to explore how the social transfer of knowledge from informed “leader” individuals enhances the performance of seasonally migratory versus resident populations. The model permits a wide range of population-level behaviors including alternative stable states, partial migration equilibria, and complex dynamics, but we focus our efforts on investigations of migration collapse mediated by a lack of informed leaders that can arise from changes in landscape structure, survivorship, reproduction, and/or social learning. Migration collapse is a hysteretic phenomenon in this model and results either in extinction of the population or purely resident behavior. The hysteretic nature of migration failure, which hinges on cultural transmission of knowledge, highlights a potentially critical role for behavior and social learning in aspects of spatial ecology and conservation biology.

Keywords Hysteresis · Migration · Leadership · Migratory movements · Population collapse · Range residency · Social learning

Introduction

Long-distance animal migrations are a striking manifestation of the interplay among behavior, ecology, and evolution. Such movements occur broadly in seasonal landscapes as complex phenomena that emerge at the population level as a result of social interactions between conspecifics and the interrelationships between individuals and elements of their environment (e.g., resources, predators). When landscapes change with respect to phenology or connectivity, the dynamics of migratory species can abruptly shift. For example, changes in climate that affect arrival times of migrating songbirds can lead to mis-timing with respect to essential resources and eventual population declines (Gordo et al. 2005; Both et al. 2006). Likewise, habitat degradation and isolation (e.g., by fencing) are believed to underlie the cessation of migration in many ungulate populations, and in such cases, the loss of migration often leads to dramatic decreases in population sizes or to local extinction of populations (Bolger et al. 2008; Newmark 2008). Such changes in movement dynamics may have extensive ecological consequences because migratory populations are often far more abundant (e.g., more than ten times) than are resident populations of the same or similar species (Fryxell et al. 1988).

The mechanisms underlying migration have been particularly well studied in birds (e.g., Alerstam 2006; Alerstam et al. 2003; Akesson and Hedenstrom 2007) and remain the subject of much current research. Evidence suggests that individuals of certain taxa may migrate alone, unaided by

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conspecifics and relying mostly on endogenous, genetically inherited programs (Berthold 2001; Wiltschko et al. 1998; Fransson et al. 2001). However, it is also clear that for many taxa, especially those that are long-lived and travel in groups, innate programs alone are not sufficient to successfully navigate migration routes (Alerstam et al. 2003). For example, in migratory southern right whales (*Eubalaena australis*), calves learn summer feeding locations from their mothers, and molecular studies suggest that culturally inherited site fidelity to feeding grounds extends over several generations (Valenzuela et al. 2009). Likewise, fawns learn migratory behavior from their mothers in northern populations of white-tailed deer (*Odocoileus virginianus*) where seasonal snow cover prohibits year-round residency (Nelson 1998). Theoretical studies indicate that animals navigate more successfully in groups and that leadership by a small number of individuals may be a key mechanism in animal navigation (Couzin et al. 2005; Guttal and Couzin 2010). Empirical studies also highlight the importance of group size for movement success. For example, experimental studies with homing pigeons found that a flock of six birds released together flew faster and straighter to their home site than did the same birds flying individually (Dell'Arciccia et al. 2008).

In systems where social factors make important contributions to movement, information transfer from more experienced individuals to inexperienced ones (e.g., juveniles) constitutes a key component of navigational success. For example, adult birds have often strikingly better navigational capabilities compared to juvenile ones, such as in white-crowned sparrows (*Zonotrichia leucophrys gambelii*) where adult birds, but not juveniles, rapidly recognize and correct for a continent-wide displacement, thereby demonstrating the importance of their learned navigational map (Thorup et al. 2007). Several studies demonstrate that adult birds need to be present for successful migration of juveniles. For example, Chernetsov et al. (2004) demonstrated for white storks (*Ciconia ciconia*) that juvenile birds, which were detained and released only after adults birds had migrated to wintering grounds, were unable to correctly navigate without the company of older birds and failed to find their winter ranges. Evidence from other bird species suggests that entire migration routes may be culturally transmitted and can be forgotten and become “extinct” in the absence of experienced (i.e., informed) individuals that can train others. In the case of whooping cranes (*Grus americana*) and Canada geese (*Branta canadensis*), migratory movements have been successfully learned using ultralight aircraft as surrogate leaders (e.g., Ellis et al. 2003). Likewise, in honey buzzards (*Pernis apivorus*), birds of different ages use different migratory routes, with adults apparently learning an efficient detour from other adults

while first year migrants (juveniles) take an alternative route involving shorter flight segments (Hake et al. 2003).

Cultural transmission of knowledge related to movement is known from non-bird taxa as well. For example, Dodson (1988) provides an extensive overview of the role of social learning for various kinds of fish movements, including diel and seasonal migrations. Particular case studies include transplant experiments with French grunts (coral reef fish; *Haemulon flavolineatum*), which demonstrated that fish can learn diel migratory routes across reef flats from experienced conspecifics (Helfman and Schulz 1984), and studies demonstrating that zebrafish (*Danio rerio*) learn escape routes from conspecifics (Lindeyer and Reader 2010). Consequently, there exists an empirical basis for expecting a connection between social learning and animal movements for diverse taxa on a variety of spatial scales.

However, the consequences of cultural transmission of migratory knowledge versus endogenous migration represents a key open topic in behavioral ecology (van Noordwijk et al. 2006), and explicit linkages among leadership, social learning, and population dynamics are only just beginning to be explored (Guttal and Couzin 2010). Here, we develop a theoretical model based on a system of difference equations to examine how individual leadership and the transmission of knowledge among individuals influence persistence in migratory populations. This work brings together ideas from models exploring the effects of resource use and habitat change on the dynamics of migratory populations (e.g., Sutherland 1996; Norris and Taylor 2006; Taylor and Norris 2007) and from individual-based models that have explored the relationship between leadership and knowledge dissemination in moving animal groups (e.g., Couzin et al. 2005; Codling et al. 2007; Sumpter et al. 2008; Guttal and Couzin 2010).

Conceptual framework

Because we are interested in populations featuring seasonal migration, we adopt a discrete time (difference equation) modeling framework that allows us to contrast the performance of migratory versus resident individuals (see also Taylor and Norris 2007). Migrants move cyclically between two patches within a year, whereas residents spend the entire year within a single patch. We have three state variables, using I_t for “informed” migrants that are familiar with the migration route and act as leaders, U_t for uninformed migrants, and R_t for resident individuals that do not migrate. The total set of migrants is $I_t + U_t$. Informed migratory individuals obtain the knowledge necessary to complete a successful migration by experience or by social learning from previously informed individuals.

Not all individuals need to learn the route, however, because a migrant may successfully navigate the migratory route if it follows what the informed individuals are doing. Benefits of informed leadership manifest through improved survivorship of uninformed migrants provided a sufficient number of leaders exist.

The model we develop using these state variables allows for a wide range of population-level behaviors including alternative stable states, coexisting stable states, and complex dynamics. Because the richness of the model's behavior precludes a concise analysis, we have opted to subdivide our investigation of the model. We focus here on a particular range of model behaviors involving a purely migratory steady state $(I,U,0)$, a purely resident steady state $(0,0,R)$, a mixed migratory-resident steady state (I,U,R) , and population extinction $(0,0,0)$. This focus allows for an investigation of migration collapse due to a lack of informed leaders together with an examination of migration collapse mediated by changes in landscape structure, survivorship, and/or reproduction. In future work, we plan to pursue the issue of how migration could evolve from a non-migratory state, which, in the present model, would require that migration be able to start when there are initially no informed individuals (see below). However, we emphasize that the evolution of migration may occur on very different timescales than the collapse of migratory populations, so it may not prove useful to treat both phenomena in a single model.

We configure our model to start at the end of the more benign of two main seasons of our model animals' annual cycle so that the migratory animals are just getting ready to depart for wintering or dry season foraging grounds with densities I_t and U_t , whereas resident animals remain in their year-long habitat at density R_t . Mortality is calculated as occurring during the harsh season, but the mortality we are concerned with includes, for migratory individuals, losses on journeys to and from breeding grounds as well as mortality during the non-reproductive stage. If we use s_M for survivorship of migratory individuals and s_R for survivorship of resident individuals, we have

$$\begin{aligned} I'_t &= s_M I_t \\ U'_t &= s_M U_t \\ R'_t &= s_R R_t, \end{aligned} \tag{1}$$

where the prime symbols (' and subsequently double primes, ") denote partial steps through an annual cycle. In another context, we will replace s_M with $s_I \neq s_U$, but initially, we assume that informed and uninformed migrants suffer the same losses to mortality. In future work that considers how migration might originally evolve, we could replace s_M in the equation for I_t with s_I and in the equation for U_t with s_U , where $s_I \neq s_U$. Here, however, we will mainly assume that informed and uninformed

migrants suffer the same losses to mortality. It is reasonable to think that the presence of larger numbers of informed individuals would increase the survival rate during migration. We can incorporate that effect into our model by replacing s_M with a term where survivorship may depend on I_t , such as $s_M \left(h + (1-h) \frac{I_t}{1+I_t} \right)$, where $0 \leq h \leq 1$ and h represents the fraction of migrants whose mortality is not influenced by the density of informed leaders. To facilitate analysis, we will generally assume that $h = 1$ so that the survival rate of migrants is independent of the number of informed individuals. However, we will also conduct numerical investigations of the case $h < 1$ to verify that our conclusions are robust relative to our assumptions about the density dependence of survivorship en route.

As discussed in the "Introduction," we study a scenario in which knowledge of "how to migrate" is socially learned rather than genetically inherited (Dodson 1988; Ellis et al. 2003; Chernetsov et al. 2004; Thorup et al. 2007; Hake et al. 2003). Given this perspective, we need to account for (i.e., update) learning among survivors of the migratory process. If the parameter l represents the probability per year of an uninformed individual "learning" how to migrate from informed conspecifics and if the parameter f represents the probability per year of an informed individual "forgetting" how to migrate, we have

$$\begin{aligned} I''_t &= (1-f)I'_t + l(I_t)U'_t = (1-f)s_M I_t + l(I_t)s_M U_t \\ U''_t &= f I'_t + (1-l(I_t))U'_t = f s_M I_t + (1-l(I_t))s_M U_t \\ R''_t &= R'_t = s_R R_t, \end{aligned} \tag{2}$$

To avoid spontaneous learning, l must depend on the density of I (with $l(0) = 0$). Similar notions underpin the emerging idea of quorum decision making in animal behavior (Ward et al. 2008). Allowing l to depend on I means that learning may occur through social mechanisms, and the strength of the dependence of l on I describes the relative importance of social interactions and experience in the way uninformed individuals become informed. In contrast, setting $l = \text{constant}$ means that uninformed individuals may learn, but only through experience. Without major changes to the system's dynamics, we can set $f = 0$ to study cases where migratory knowledge, once learned, cannot be forgotten by an individual.

Following the arrival of migrating individuals to the breeding grounds (where they rejoin the year-long resident portion of the population), reproduction occurs. To model reproduction, we use a generalized Beverton–Holt formulation that allows migrating and resident individuals to differ in *both* their respective reproductive rates (denoted by ρ_M and ρ_R) and their respective sensitivities to crowding/resource competition (denoted

by b_M and b_R), yielding,

$$N_{t+1} = I_t'' + U_t'' + R_t'' + \frac{\rho_M(I_t'' + U_t'') + \rho_R R_t''}{1 + b_R R_t'' + b_M(I_t'' + U_t'')} \quad (3)$$

Following reproduction, the next step in the life cycle is (for those individuals that migrate) migration back to the harsh season habitat. However, in this model, the distinction between resident and migratory individuals is neither innate nor genetically determined. Instead, we model the distinction as a consequence of social behavior, with individuals making a decision to migrate based, at least in part, on the presence of informed leaders, such as in many long-lived species (e.g., cranes, stork, or geese; Sutherland 1998; van Noordwijk et al. 2006; Pulido 2007). To capture this phenomenon, we introduce the function $g(I)$, which can be thought of as the “persuasiveness” of the informed leaders, yielding,

$$\begin{aligned} I_{t+1} &= I_t'' \\ U_{t+1} &= g(I_t'')(N_{t+1} - I_t'') \\ R_{t+1} &= [1 - g(I_t'')](N_{t+1} - I_t'') \end{aligned} \quad (4)$$

Because of its importance to the dynamics of the overall system, we want to keep $g(I)$, which is constrained such that $0 \leq g(I) \leq 1$, as general as possible for the purposes of analyzing the equations. Nevertheless, we can point out some options for $g(I)$ here that will be important for scenarios considered later in the paper. For example, if we set $g(0) = 0$, we have a situation where, without any informed individuals, migration ceases. In contrast, if we set $g(0) > 0$, we allow recruitment (in a joint behavioral-reproductive sense) from R into U , a scenario which will be explored in another paper. In general, we will treat $g(I)$ as an increasing but saturating function of I . This captures the importance of “concentration of knowledge” for compelling transitions from resident to migratory groups or vice versa. Note that in using Eq. 4, we do not discriminate between adults and recently born individuals with respect to the opportunity to migrate or remain resident. An alternative form would have young of the year (e.g., calves) follow their mothers.

Analyses of the model

Standard linearization techniques together with some involved algebra can be used to assess the existence and stability of equilibria for the model represented in Eqs. 1–4 (see Appendix). In all of the cases we consider, we assume $f = 0$ and $g(0) = 0$, and for some calculations in the Appendix, we assume the forms of parameter dependence shown in this section. For most of the analysis and

discussion, we will assume that the survival rate of migrants is a constant, s_M , but in some cases, we will also examine what happens when survival depends on I .

Existence and characterization of equilibria

The model always admits the extinction equilibrium (0,0,0). If $s_R + s_R \rho_R < 1$, this extinction equilibrium is stable. However, at $s_R + s_R \rho_R = 1$, a transcritical bifurcation occurs in which the stability of the extinction equilibrium is lost and the all-resident state, $(0, 0, R_1^*)$, where $R_1^* = \frac{s_R(1+\rho_R)-1}{b_R s_R(1-s_R)}$, emerges as a stable equilibrium. In biological terms, survival and reproduction must be sufficiently strong to maintain a stable all-resident population. Note that R_1^* is used to distinguish this equilibrium from a coexisting equilibrium (discussed below) and that, from above, having $(0, 0, R_1^*)$ as a possible equilibrium requires $g(0)=0$. Mathematical analyses demonstrating these points appear in the Appendix.

Existence of additional stable fixed points can be explored numerically. For convenience at this point, we aggregate all the substage dynamics into a single system of equations and eliminate the notation involving primes, yielding:

$$\begin{aligned} I_{t+1} &= (1 - f)s_M I_t + l(I_t)s_M U_t \\ U_{t+1} &= g(I_{t+1})K_{t+1} \\ R_{t+1} &= (1 - g(I_{t+1}))K_{t+1} \end{aligned} \quad (5)$$

where

$$\begin{aligned} K_{t+1} &= f s_M I_t + (1 - l(I_t))s_M U_t + s_R R_t \\ &+ \frac{\rho_M s_M (I_t + U_t) + \rho_R s_R R_t}{1 + b_M s_M (I_t + U_t) + b_R s_R R_t} \end{aligned} \quad (6)$$

In what follows, we will take $f=0$. Furthermore, to explore parameter space numerically, we assume explicit but parameter-sparse forms for the learning and persuasiveness functions. For learning, we use

$$l(I_t) = \frac{l_1 I_t}{1 + l_1 I_t} \quad (7)$$

which means that the probability that an uninformed individual opts not to migrate will decline as the density of informed migrants increases. The reason for this is that Eq. 7 implies that a larger I means a larger fraction of U_t go into I_{t+1} and hence migrate; the remaining fraction of U_t is more likely to move into U_{t+1} as I increases because of our assumption that $g(\cdot)$ increases with I . This setup accords well with empirical results regarding the importance of density (alternatively, group size) for effective transfer of information related to group movement (Conradt and Roper 2005; Ward et al. 2008).

For persuasiveness, we consider two alternative cases. Though seeming similar at first glance, these two cases lead to fundamentally different results concerning the nature of the equilibria that include migratory forms. Specifically, one case leads to a “partial migration” scenario in which migrants and residents coexist, whereas the other case leads to a purely migratory scenario. In case 1, we set

$$g(I_{t+1}) = \frac{g_1 I_{t+1}}{1 + g_1 I_{t+1}}, \tag{8}$$

so that persuasiveness merely asymptotes toward (but never actually reaches) $g = 1$ as the number of informed individuals increases. In case 2, we set a threshold density I_c , above which leaders are perfectly persuasive, yielding

$$g(I_{t+1}) = \begin{cases} I_{t+1}/I_c & I_{t+1} < I_c \\ 1 & I_{t+1} \geq I_c \end{cases}. \tag{9}$$

For both cases 1 and 2, a stable equilibrium featuring migratory individuals (I_2^*, U_2^*, R_2^*) can coexist with a stable residents-only equilibrium $(0, 0, R_1^*)$ over a wide range of parameter space. In case 1, where $g(I)$ never reaches 1 (Eq. 8), a stable I_2^*, U_2^*, R_2^* equilibrium with I_2^*, U_2^* , and R_2^* all positive may exist, where

$$\begin{aligned} U_2^* &= g_1 I_2^* R_2^* \\ I_2^* &= \frac{1-s_M}{h_1 (s_M (g_1 R_2^* + 1) - 1)} \end{aligned}, \tag{10}$$

and R_2^* is a positive real root of a quartic polynomial. Thus, case 1 corresponds to a partial migration in which both resident and migratory individuals exist within a single population (Lundberg 1988; Taylor and Norris 2007). Note that having a positive value for I_2^* requires that $s_M (g_1 R_2^* - 1) > 1$, which will be true if s_M is sufficiently close to 1.

To examine the effects of density-dependent survival of migrants, we can replace s_M with $s_M \left(h + (1-h) \frac{I_t}{1+I_t} \right)$. For large I_t , this expression approaches s_M , and dynamics in the modified model are well approximated by the original model. For small I_t , this expression approaches $h s_M \leq s_M$. With density-dependent survival of migrants, the $(0, 0, R_1^*)$ equilibrium remains unchanged. However, the (I_2^*, U_2^*, R_2^*) equilibrium becomes

$$\begin{aligned} U_2^* &= g_1 I_2^* R_2^* \\ I_2^* &= \frac{1-s_M + h_1 (1-h s_M (1-g_1 R_2^*)) \left(1 + \sqrt{1 + \frac{4h_1 (1-h s_M) (s_M (1+g_1 R_2^*) - 1)}{(1-s_M + h_1 (1-h s_M (1-g_1 R_2^*))^2)}} \right)}{2h_1 (s_M (g_1 R_2^* + 1) - 1)}, \end{aligned} \tag{11}$$

and R_2^* is a positive real root of a sixth order polynomial. There is also a potential (I_3^*, U_3^*, R_3^*) equilibrium, but numerical work suggests that the I_3^* root is always negative.

To examine the population-level consequences of migratory collapse, we are interested in the quantity

$$\xi = \frac{U_2^* + I_2^*}{R_1^*}, \tag{12}$$

which reports the ratio of the migratory portion of the pre-collapse population to the wholly resident post-collapse population.

Alternatively, for case 2 where $g(I) = 1$ for large I (Eq. 9), the stable (I_2^*, U_2^*, R_2^*) equilibrium is the purely migratory case $(I_2^*, U_2^*, 0)$, and stable migratory equilibria, if they exist, are given by

$$\begin{aligned} U_2^* &= \frac{\rho_M}{b_M} + \left(1 - \frac{l_1}{b_M s_M} \right) \frac{1-s_M}{l_1}, \\ I_2^* &= \frac{s_M (1+\rho_M) - 1}{b_M (1-s_M)} - \frac{1-s_M}{l_1}, \end{aligned} \tag{13}$$

where

$$U_2^* + I_2^* = \frac{s_M (1 + \rho_M) - 1}{b_M s_M (1 - s_M)}. \tag{14}$$

The ratio of the density of the purely migratory equilibrium to that of the purely resident one is

$$\xi = \frac{s_M (1 + \rho_M) - 1}{s_R (1 + \rho_R) - 1} \frac{b_R s_R (1 - s_R)}{b_M s_M (1 - s_M)}. \tag{15}$$

The scenario in Eqs. 13–15 presents an analytically tractable case in which the population-level consequences of migration collapse can be studied to gain insight into the more general case in Eqs. 10 and 12.

Bifurcation dynamics and the collapse of migratory populations

A stable (I_2^*, U_2^*, R_2^*) equilibrium with $I_2^*, U_2^* > 0$ may lose stability if parameters relevant to the migratory subpopulation dynamics pass a critical threshold. In this manner, our model predicts the potential for a catastrophic collapse of a population that is wholly or partially migratory. Following the collapse of migration, a population will converge on one of two possible stable fixed points: extinction, $(0, 0, 0)$, or purely resident behavior, $(0, 0, R_1^*)$ (see Appendix for mathematical details).

For case 1, where $g(I)$ asymptotes as the density of informed leaders increases (Eq. 8), consider the scenario $\rho_M = 0.75$, $\rho_R = 1.0$, $b_M = b_R = 1.0 \times 10^{-3}$, $g_1 = 1.0$, $s_M = 0.9$, and $s_R = 0.65$. Because $\rho_M < \rho_R$ and $s_M > s_R$, the migratory subpopulation has a disadvantage in reproduction but an advantage in survivorship. The remaining parameter, l_1 , which we allow to vary, appears in Eq. 7. At higher values of l_1 , the probability of learning increases more rapidly with the number of informed individuals. In Fig. 1, for each equilibrium, we plot, separately, the dependence of I_2^*, U_2^* ,

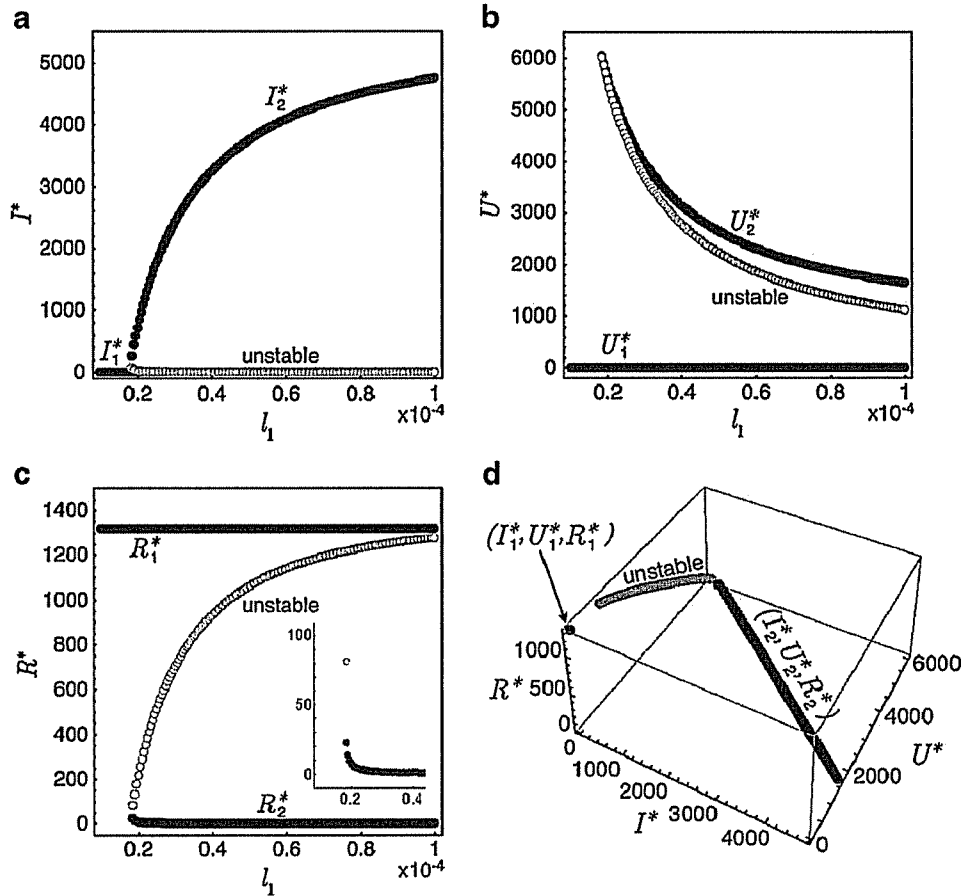


Fig. 1 Equilibrial abundances of the informed (I), uniformed (U), and resident (R) forms of the model species for case 1 (persuasiveness saturates with density of informed migrants) with $\rho_M=0.75$, $\rho_R=1.0$, $b_M=b_R=1.0 \times 10^{-3}$, $g_1=1.0$, $s_M=0.90$, and $s_R=0.65$. For each equilibrium, the dependence of the I^* (a), U^* (b), and R^* (c) population components are plotted separately as functions of l_1 . Note that $R_2^* > 0$ for small values of l_1 , meaning that in this case, the model allows for a transition between pure resident and partial migration scenarios

and R_2^* on l_1 . If l_1 falls below a critical threshold, the nontrivial stable equilibrium, where migratory and resident subpopulations coexist, will lose stability, and demographic fluctuations will precipitate a collapse of migration. The source of this threshold behavior is a saddle-node bifurcation, as shown in Fig. 1d where the equilibria are plotted in the (I_2^*, U_2^*, R_2^*) phase space with l_1 as an implicit parameter.

Likewise, in case 2, if we use Eq. 9, where a threshold density of informed leaders exists, the bifurcation can occur when a sufficiently large change in one of several parameters (s_M, ρ_M, b_M or l_1) pushes $I_2^* < I_c$. That a bifurcation event can be triggered by multiple parameters means that changes in local demography, landscape changes en route, or factors affecting social learning may all trigger the cessation of migration. Specifically, the bifurcation and corresponding migratory collapse can occur given a sufficient decrease in

(where I_2^*, U_2^* and R_2^* are all positive; see inset in c). Note further that R_2^* depends on many parameters and can assume much larger values than in this scenario. In d, the equilibria are plotted with l_1 as an implicit parameter. The $(0, 0, R_1^*)$ stable fixed point is independent of l_1 and appears as a single, isolated black dot. In contrast, the coexisting (I_2^*, U_2^*, R_2^*) equilibrium depends on l_1 and sweeps out a curve as l_1 is varied. Dots corresponding to stable (black) and unstable (gray) fixed points are shown

reproductive output (ρ_M), an increased sensitivity to crowding (b_M), an increase in the hostility of the landscape over which migration must occur (decreasing s_M), or an evolutionary or behavioral reduction in the ability of uninformed individuals to learn how to migrate given experience (l_1). In each situation, the destabilization of the $(I_2^*, U_2^*, 0)$ equilibrium and subsequent collapse of the migratory population to a purely resident population is ultimately tied to the absence of a critical density of informed leaders necessary to persuade all of the uninformed individuals to migrate (Fig. 2).

Within each of cases 1 and 2, the qualitative dynamics of the model are robust to changes in the parameters $\rho_M, \rho_R, b_M, b_R, g_1, s_M, s_R$, and l_1 provided that these changes do not violate the criteria for existence of equilibria (defined above). For example, bifurcation plots for cases where migrants have lower survival but higher reproduction than

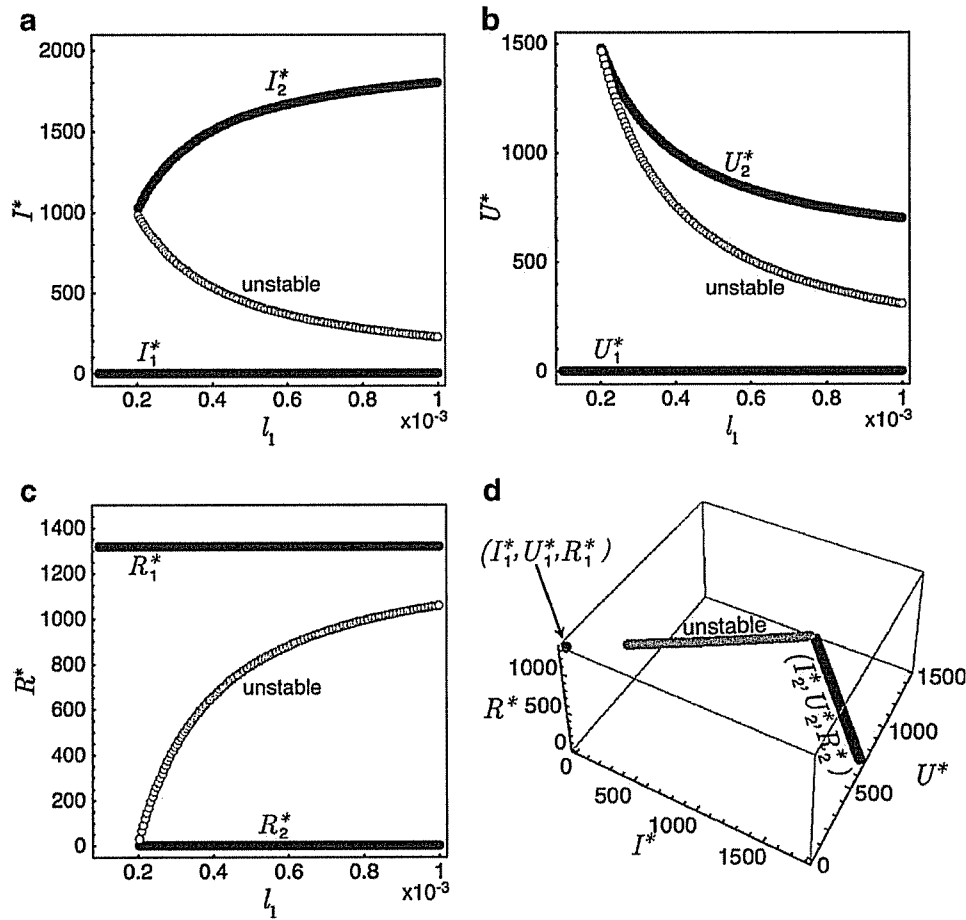


Fig. 2 Equilibrial abundances of the informed (I), uniformed (U), and resident (R) forms of the model species for case 2 (persuasiveness of informed migrants is complete above a threshold density I_0) with $\rho_M=0.75$, $\rho_R=1.0$, $b_M=b_R=1.0 \times 10^{-3}$, $I_0=1,000$, $s_M=0.80$, and $s_R=0.65$. For each equilibrium, the dependence of the I^* (a), U^* (b), and R^* (c) population components are plotted separately as functions of l_1 . Note that $R_2^*=0$ for all values of l_1 , meaning that this model allows for a

transition between pure resident and pure migration scenarios, with no possibility of partial migration. In d, all three equilibria are plotted with l_1 as an implicit parameter. The $(0, 0, R_1^*)$ stable fixed point is independent of l_1 and appears as a single, isolated black dot. In contrast, the coexisting (I_2^*, U_2^*, R_2^*) equilibrium depends on l_1 and sweeps out a curve as l_1 is varied. Dots corresponding to stable (black) and unstable (gray) fixed points are shown

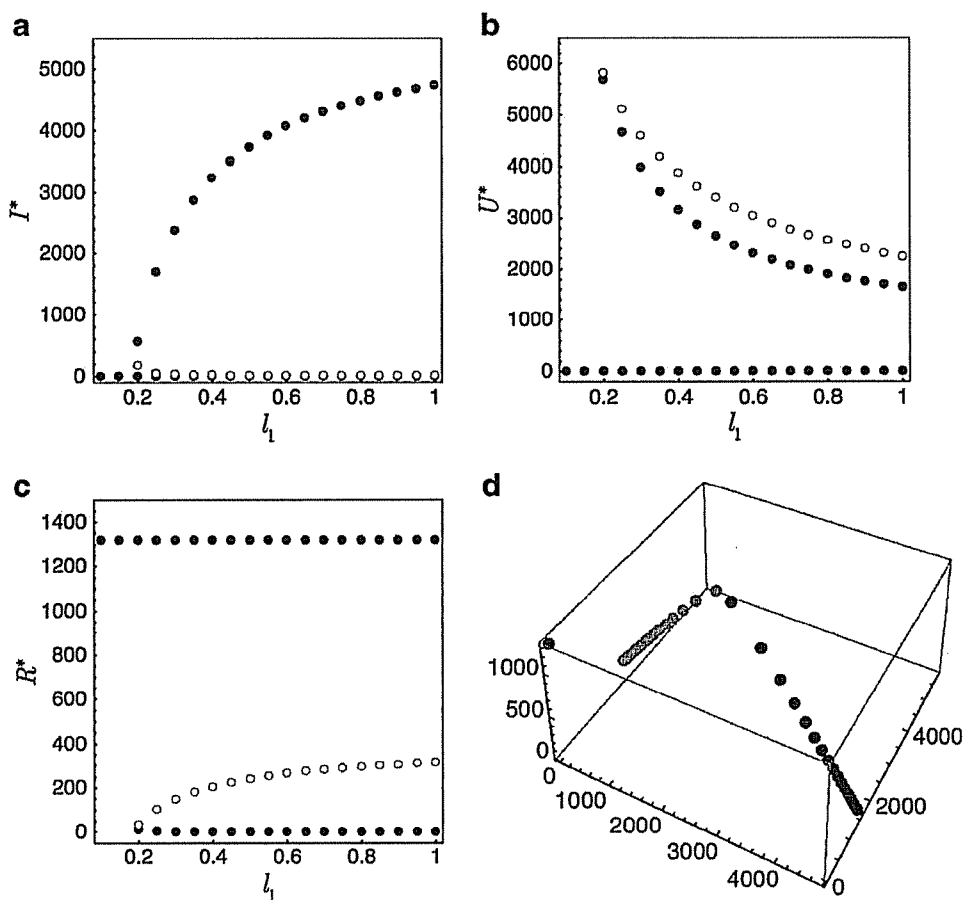
residents are comparable to those appearing in Figs. 1 and 2 where the trade-off is reversed (results not shown).

Allowing the survival of migrants to depend upon the density of informed individuals does not qualitatively alter the model's dynamics. In Fig. 3, we plot bifurcations from Eq. 11 using the same parameters as in Fig. 1, with the addition that $h = 0.25$. All plotted values of I_2^* are fairly large, so the (I_2^*, U_2^*, R_2^*) branch matches the results in Fig. 1, as expected. Along the unstable branch, I_2^* is small, and in this case, U_2^* and R_2^* differ quantitatively from our original results. Overall, predictions about system dynamics are robust relative to the dependence of s_M on I_t and are also robust relative to the values of parameters.

Because migratory species are often staggeringly abundant in the real world (e.g., Fryxell et al. 1988), it is of great interest to explore the factors controlling the relative

densities of migratory and resident populations in this model. This issue is particularly interesting in the context of the saddle-node bifurcation in which decreases in ρ_M or s_M (interpretable as progressive degradation in resource availability or decreased survivorship while migrating) are some of the mechanisms that can lead to the elimination of migratory individuals. In both cases 1 and 2, the density of the migratory population $I_2^* + U_2^*$ from the stable (I_2^*, U_2^*, R_2^*) equilibrium can be either greater than or less than the density of the resident population from the stable $(0, 0, R_1^*)$ population that persists after the catastrophe. Increases in s_M , and especially increases in s_M relative to s_R , lead to large values of ξ in which the migratory population is far more abundant than the resident population that persists following the collapse of migration (Fig. 4).

Fig. 3 Equilibrial abundances of the informed (I), uniformed (U), and resident (R) forms of the model species for case 1 (persuasiveness saturates with density of informed migrants) with $\rho_M=0.75$, $\rho_R=1.0$, $b_M=b_R=1.0 \times 10^{-3}$, $g_1=1.0$, $s_M=0.90$, and $s_R=0.65$, but now allowing for the survival of migrants to depend on the density of informed leaders (Eq. 11 with $h=0.25$). For each equilibrium, the dependence of the I^* (a), U^* (b), and R^* (c) population components are plotted separately as functions of l_1 . In d, the equilibria are plotted with l_1 as an implicit parameter. The $(0, 0, R_2^*)$ stable fixed point is independent of l_1 and appears as a single, isolated *black dot*. In contrast, the coexisting (I_2^*, U_2^*, R_2^*) equilibrium depends on l_1 and sweeps out a curve as l_1 is varied. Dots corresponding to stable (*black*) and unstable (*gray*) fixed points are shown



Discussion

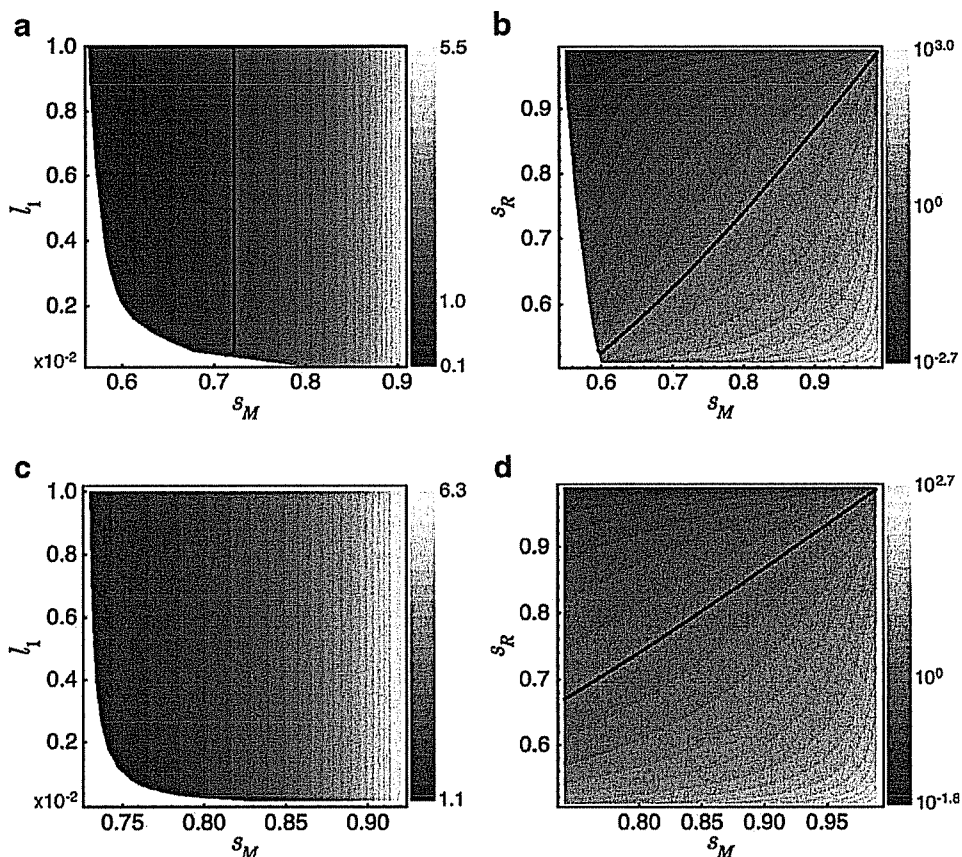
Previous models examining the interplay between resident and migratory populations, such as Sutherland (1996), Norris and Taylor (2006), and especially Taylor and Norris (2007), have all noted the important roles that demographic factors can play in shifting the relative abundance of migratory and resident forms. In those models, shifts in the relative reproductive rates and survivorship of resident and migratory forms can shift a population from an all-resident scenario to an all-migratory scenario by passing through a partial migration scenario featuring both types of individuals. A key difference in our model is that we do not assume that migration is strictly genetically determined, but instead focus on cultural transmission of knowledge as a key component for successful migration.

Two key aspects of this cultural transmission of knowledge are worth emphasizing. First, the seemingly subtle issue of whether the persuasiveness of informed leaders at high density is “complete” or merely “very high” has a qualitative impact on the model’s output, controlling whether the equation system allows pure migration or partial migration. Second, our emphasis on cultural transmission leads directly to scenarios in which migration

failure is a hysteretic phenomenon. In our modeling framework, a decrease in survivorship during migration (or one of several other key parameters) will still switch the system from a purely or partly migratory state (I_2^*, U_2^*, \cdot) to a purely resident state $(0, 0, R_1^*)$. However, the change in state is hysteretic, and it is not possible to regain the migratory component simply by improving survivorship en route once the population has collapsed to an all-resident stable state. Instead, some additional factors would also need to change as well, such as invoking some external management strategy that provided a fresh source of migratory individuals for the population allowing $I > 0$.

Our model indicates that a reduction in survivorship during migration beyond a critical threshold will yield a collapse of the migratory (or part-migratory) population to a purely resident one. Under certain conditions, the switch from a migratory population to an all resident population will be accompanied by a large decline in population size (Fig. 4). This type of process has been observed repeatedly in real-world ungulate populations where the loss of migration leads to dramatic decreases in population sizes (Bolger et al. 2008; Newmark 2008). Similar processes seem to operate in some populations of migratory fish where low per capita resource availability is often a trigger

Fig. 4 Contour plots giving examples of the parameter dependence of the ratio ξ that characterizes the relative abundance of the resident and migratory populations. In **a** and **c**, corresponding to case 1 and case 2, respectively, contours of ξ are drawn over the region where stable (I_2^*, U_2^*, R_2^*) equilibria exist in the l_1, s_M plane. In **b** and **d**, corresponding to case 1 and case 2, respectively, contours of $\log_{10} \xi$ are drawn over the region where stable (I_2^*, U_2^*, R_2^*) equilibria exist in the s_R, s_M plane. *Black lines* mark points where $\xi=1$ (a *black line* does not appear in **c** because all contours correspond to $\xi>1$). Case 1 parameters: $\rho_M=0.75, \rho_R=1.0, b_M=b_R=1.0 \times 10^{-3}$, and $g_1=1$, with $s_R=0.65$ for **a** and $l_1=0.005$ for **b**. Case 2 parameters: $\rho_M=0.75, \rho_R=1.0, b_M=b_R=1.0 \times 10^{-3}$, and $I_0=1,000$, with $s_R=0.65$ for **c** and $l_1=0.005$ for **d**



for migratory phenotypes in populations with partial migration (Olsson et al. 2006). For example, following the construction of river dams that prevent migration, residual populations of char (*Salvelinus leucomaenis*) upstream from the dams switch from a migratory life history to a resident one, a change that appears linked to the low density conditions that occur following the cessation of migration (Morita et al. 2000).

This manuscript should be viewed as only an initial step in the direction where leadership, social learning, genetics, and population dynamics will eventually be linked in a single model (for a complementary approach using individual-based models, see Guttal and Couzin 2010). Nevertheless, the model we introduce here is sufficiently general that it will permit a wide variety of subsequent investigations into interesting aspects of migratory movements. In particular, changes to the existing functional form of $g(\cdot)$, the introduction of structure within the informed subpopulation, or the introduction of density dependence in any of several places would lead to models with strikingly different interpretations from the current formulation and, in concert, the potential for a wider range of population dynamics. For example, if we allow $g(0) \neq 0$, the model generalizes to include cases where there could be spontaneous development of migration. Such a change would represent natural selection favoring individuals that are able to migrate successfully in the absence of informed leaders

and thereby become informed through experience rather than social learning. However, such a change also disallows $(0, 0, R_1^*)$ as a stable equilibrium. Likewise, if we rewrote $g(\cdot)$ so that persuasiveness depends not just on the availability of informed leaders but also on the density of resident individuals (i.e., $g \equiv g(I, R)$, where the dependence on R is interpreted to relate to crowding relative to available resources), we have a model wherein the interplay between local resource conditions and future opportunities in a distant locale could be considered. Such a model would allow for a direct examination of model transitions from explicit territoriality to migratory movements. Moreover, dividing the informed subpopulation on the basis of age (with corresponding changes to the functions $g(\cdot)$ and (\cdot)) would permit an examination of how experience gained over multiple migratory roundtrips influenced population dynamics. This could be especially interesting in conjunction with the adoption of density dependence in survival during migration (i.e., $s_M \equiv s_M(I)$, as in Eq. 11 and Fig. 3). In particular, allowing s_M to depend on I but setting $s_M(0) > 0$ can be interpreted as allowing for the existence of exploratory dispersal in the absence of informed leaders and could permit the existence of additional equilibria (e.g., $(0, U^*, 0)$ or $(0, U^*, R^*)$) that would be indicative of different population-level movement strategies. Perspectives such as these are explicitly evolutionary in nature because the

density-dependent behaviors would likely be shaped by natural selection in that a migration trip could be more dangerous, time-consuming, or energetically demanding when led by fewer informed individuals.

To explore the interplay between residency and migratory movements from an altogether different vantage point, one could develop a model that explicitly included population genetics (see also Griswold et al. 2010; Blanquart and Gandon 2011). Of particular interest would be an exploration of how interbreeding between resident and migratory forms results in new individuals of either (or both) types as a function of environmental conditions. Such a model, which would likely lead to rather different population dynamics and conditions for the maintenance of migration than that afforded by cultural transmission of behavior, will be explored in future work.

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Appendix

Mathematical analyses providing the conditions for existence of alternative steady states

Basic features of the model and non-migratory equilibria

It is clear that (0,0,0) is always an equilibrium for 5 and 6. Recall that we assume $g(0) = 0$ and $l(0) = 0$, but $g(I) > 0$ and $l(I) > 0$ for $I > 0$ in the cases we consider. In that case, the model may have additional equilibria of the forms (0,0, R^*), (I^* , U^* , 0), or (I^* , U^* , R^*), depending on parameter values, but it cannot have any other types of equilibria. For example, if $I^* = 0$, then by 4, $U^* = 0$, so no equilibrium of the form (0, U^* , R^*) is possible. Other forms of equilibria can be ruled out by similar arguments. If the system is linearized around (0,0,0), the eigenvalues for the linearized system are 0, $s_M(1 - f)$, and $s_R + s_R\rho_R$. Thus, if $s_R + s_R\rho_R < 1$, the equilibrium (0,0,0) is stable, and if $s_R + s_R\rho_R > 1$, it is unstable. The eigenvector corresponding to $s_R + s_R\rho_R$ is (0,0,1), so if (0,0,0) is unstable, the instability is with respect to R .

The set $\{(0, 0, R) : R \geq 0\}$ is invariant if $g(0) = 0$. If $I = U = 0$, then R satisfies

$$R_{t+1} = s_R R_t + \frac{\rho_R s_R R_t}{1 + b_R s_R R_t}, \tag{16}$$

which has a unique nonzero equilibrium $R^* = \frac{s_R(1+\rho_R)-1}{b_R s_R(1-s_R)}$ that is positive if and only if $s_R + s_R\rho_R > 1$. The model behaves like a Beverton–Holt model, so that if $R^* > 0$, then R^* is globally stable among positive solutions of relative to the set $\{(0, 0, R) : R \geq 0\}$. In that case, (0,0, R^*) is an equilibrium

for the full system. The equilibrium (0,0, R^*) can be viewed as arising from (0,0,0) via a transcritical bifurcation in a manner similar to the bifurcation of a positive equilibrium from zero in the Beverton–Holt model. Such a bifurcation occurs when the equilibrium (0,0,0) becomes unstable, which happens when the quantity $s_R + s_R\rho_R$ increases from $s_R + s_R\rho_R < 1$ to $s_R + s_R\rho_R > 1$. The eigenvalues for the linearization around (0,0, R^*) can be computed to be 0, $s_M(1 - f)$, and $1 - (1 - s_R)\left(\frac{b_R s_R R^*}{1 + b_R s_R R^*}\right)$, which are all < 1 in magnitude, so that the equilibrium (0,0, R^*) is stable if $R^* > 0$. Some algebra shows that to have the third eigenvalues < 1 is equivalent to $s_R + s_R\rho_R > 1$, so the (0,0, R^*) equilibrium becomes stable precisely where (0,0,0) loses stability, which is where the transcritical bifurcation occurs (note that if $g(0) \neq 0$, then any equilibrium with $I^* = 0$ and $R^* > 0$ must have $U^* > 0$, so that no equilibrium of the form (0,0, R^*) can exist).

Migratory equilibria

To see when 5 and 6 have an equilibrium with I^* and U^* positive, first note that $N = I + U + R$ satisfies

$$N_{t+1} \leq sN_t + \frac{\rho s N_t}{1 + b s N_t} \tag{17}$$

where $s = \max\{s_M, s_R\}$, $\rho = \max\{\rho_M, \rho_R\}$, and $b = \min\{b_M s_M/s, b_R s_R/s\}$. It follows that if $s + s\rho > 1$, then for large t , we have $N_t \leq \bar{N} + 1$, where $\bar{N} = \frac{s+s\rho-1}{bs(1-s)}$ is the unique positive equilibrium of 17 if the inequality is replaced by equality (see Cosner 1996). If $s + s\rho < 1$, then 17 implies that all solutions of the original model go to zero as t goes to infinity. Hence, N is uniformly bounded as long as the parameters of the model are restricted to some finite set. Suppose that $g(I) \leq g_0 I$ for some g_0 when $I \geq 0$ (this is true for all the cases we consider). Then for any positive equilibrium, we have $I^* \leq s_M(I^* + U^*) \leq s_M(1 + g_0 \bar{N})I^*$. It follows that if s_M is too small, the model cannot have any equilibria with I^* positive.

If $g(I) = 1$ for I large, then the model may have an equilibrium of the form ($I^*, U^*, 0$). If so, then $P^* = I^* + U^*$ satisfies $P^* = s_M P^* + \frac{\rho_M s_M P^*}{1 + b_M s_M P^*}$ so that $I^* + U^* = P^* = \frac{s_M(1+\rho_M)-1}{b_M s_M(1-s_M)}$, as in 13. Note that this requires $s_M(1 + \rho_M) > 1$. If $f = 0$ (no forgetting) and $l(I) = \frac{l_1 I}{1 + l_1 I}$ as in 7, then using $U^* = P^* - I^*$ in the first equation of 5 allows the explicit calculation of I^* and U^* as in 12. If $l_1 > \frac{b_M(1-s_M)^2}{s_M(1+\rho_M)-1}$, this yields a positive value for I^* . If $g(I)$ is defined as in 9 and it turns out that $I_c < \frac{s_M(1+\rho_M)-1}{b_M(1-s_M)} - \frac{1-s_M}{l_1}$, then the values of I^* and U^* shown in 12 correspond to an actual equilibrium of the model. The specific form of $l(I)$ given in 7 is not essential for the existence of an (I^*, U^* , 0) equilibrium, but it is natural and facilitates calculation.

If the model is linearized around an $(I^*, U^*, 0)$ equilibrium, then the eigenvalues turn out to be 0, $s_M I(I^*)$, and $s_M - s_M I(I^*) + (1 - s_M)^2 / s_M \rho_M$. Clearly, the first two of these are less than one in magnitude. Since $I(I^*) < 1$, the third is positive, and since $s_M(1 + \rho_M) > 1$, it follows that $(1 - s_M) / s_M \rho_M < 1$, so $s_M - s_M I(I^*) + (1 - s_M)^2 / s_M \rho_M < 1 - s_M I(I^*) < 1$. Thus, in the situation treated in this paper, any $(I^*, U^*, 0)$ equilibrium must be stable.

We have seen that the model admits a global bound on all populations when the parameters are restricted to any finite set. Furthermore, there are no equilibria with I^* or U^* positive if s_M is too small, and the nature of the stabilities or instabilities of the linearizations at $(0, 0, 0)$ and $(0, 0, R^*)$ as measured by number of eigenvalues ≥ 1 in absolute value do not change as s_M is varied. On the other hand, there are values of the other parameters such that if s_M is large then stable $(I^*, U^*, 0)$ equilibria must exist. These observations suggest that it may be possible to construct an argument based on fixed point indices or degree theory that would show that if stable equilibria appear when s_M is increased then unstable equilibria must also appear. We have not attempted to do so, but numerical computations are consistent with such behavior. Specifically, the numerical examples appear to show saddle-node bifurcations, which are the simplest way in which new equilibrium solutions can arise without changing the degree of the mapping that defines the equilibria relative to a large set determined by the a priori bounds on populations.

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