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Ideal Free Distributions, Evolutionary Games, and Population Dynamics in Multiple-Species Environments

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ABSTRACT: In this article, we develop population game theory, a theory that combines the dynamics of animal behavior with population dynamics. In particular, we study interaction and distribution of two species in a two-patch environment assuming that individuals behave adaptively (i.e., they maximize Darwinian fitness). Either the two species are competing for resources or they are in a predator-prey relationship. Using some recent advances in evolutionary game theory, we extend the classical ideal free distribution (IFD) concept for single species to two interacting species. We study population dynamical consequences of two-species IFD by comparing two systems: one where individuals cannot migrate between habitats and one where migration is possible. For single species, predator-prey interactions, and competing species, we show that these two types of behavior lead to the same population equilibria and corresponding species spatial distributions, provided interspecific competition is patch independent. However, if differences between patches are such that competition is patch dependent, then our predictions strongly depend on whether animals can migrate or not. In particular, we show that when species are settled at their equilibrium population densities in both habitats in the environment where migration between habitats is blocked, then the corresponding species spatial distribution need not be an IFD. Thus, when species are given the opportunity to migrate, they will redistribute to reach an IFD (e.g.,

under which the two species can completely segregate), and this redistribution will also influence species population equilibrial densities. Alternatively, we also show that when two species are distributed according to the IFD, the corresponding population equilibrium can be unstable.

Keywords: adaptive foraging, competition, evolutionarily stable strategy, habitat choice, ideal free distribution, predator-prey, replicator system.

A central challenge in ecology is to develop models that faithfully capture those important mechanistic details of natural systems that are required to make reliable predictions about population dynamics. We have long known that factors such as food, predators, and the densities of conspecifics and heterospecifics have important effects on population dynamics of species. It is also recognized that these aggregate population characteristics ultimately depend on the behaviors of individuals. The evidence for these facts comes from two largely independent research programs: population ecology and evolutionary ecology. While the basic unit population ecology focuses on is a population, evolutionary ecology focuses on the individual. Despite the progress in these two lines of research, population biologists rarely explicitly integrate the behavior of individuals into their models, and/or evolutionary ecologists rarely consider the consequences that the individual behavior they study has on population dynamics.

There is a growing sense that these two independent lines of research should be integrated in order to develop a complete understanding of how predators and intra- and interspecies interactions affect population demography and dynamics (Rosenzweig 1991; Levin 1992; Werner 1992; Abrams 1995; Sutherland 1996; Fryxell and Lundberg 1997; Bolker et al. 2003). Indeed, this integration is viewed as critical. If the mechanistic details at the level of individual behavior are key to population dynamics, then ecologists will have considerable difficulty predicting population and community dynamics using conventional models that do not account for this added detail.

In this article, we want to illustrate that both research programs can be integrated within the framework of pop-

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ulation game theory. In contrast to classical game theory, population game theory considers both individual behavior (i.e., individual timescale) and population dynamics (i.e., population timescale). To show some recent developments in this direction, we will consider the interplay between migration in habitat environments and population dynamics in multispecies environments. The original concept of ideal free distribution (IFD; Fretwell and Lucas 1970) considers a single species whose individuals are free to settle in any habitat and have a complete knowledge about the quality of each habitat. It is a purely behavioral concept because it does not consider the effect of changing population size. If resources are immediately consumed on their arrival in the system, then Parker (1978) derived the "input matching rule," which states that the ratio of resource input rates "matches" the consumer distribution across occupied habitats (see also Parker and Stuart 1976; Milinski and Parker 1991; Sutherland 1996). The concept of IFD for a single population was also extended to situations where either consumers and/or resources undergo population dynamics (Lessells 1995; Křivan 1997; van Baalen et al. 2001). It has also been extended to two-species environments where the two species are either competing for resources (Lawlor and Maynard Smith 1976; Brown 1990, 1998; Possingham 1992; Grand and Dill 1999; Grand 2002; Guthrie and Moorhead 2002; Křivan and Sirot 2002; Křivan 2003) or are in the predator-prey interaction (Křivan 1997; Křivan and Schmitz 2003).

There is no doubt that the IFD is a game-theoretic concept because the individual fitness depends on the distribution of other con- and heterospecific individuals. The crucial concept of evolutionary ecology is that of evolutionarily stable strategies (ESS; Maynard Smith 1982). One aim of this article is then to use the ESS to predict stability at either the individual or the population timescale level. We do this by comparing two systems. In one system, animals do not migrate between patches (i.e., every animal spends all its lifetime in a single patch) while in the other, they do migrate. We start to analyze the two-habitat, single-species system in the framework of evolutionary game theory. As defined, under the IFD, each individual must have the same fitness, and no other behavioral type using a different strategy can do better. From this perspective, the above description of an IFD corresponds to a Nash equilibrium (NE) of the game. However, an NE may not be stable with respect to either newly arising invaders that play a different strategy or spatial perturbations in species distribution. Because these basic concepts are similar in many aspects, it is important to show in which sense, and if at all, the IFD is stable. We do this at both the individual timescale level and the population timescale level.

The main conclusion of this single-species analysis is

that the stability of the system is unaffected by individual behavior (i.e., whether animals stay all their life in a single habitat or move between the two). This is true for the single-species habitat selection model even if there are multiple (i.e., more than two) habitats. This may explain why the game-theoretic method has received little attention in the literature where the IFD for single-species habitat systems predominate.

On the other hand, we go on to show that it is important to know whether an individual spends all of its time in one habitat or migrates between them when there are two species. First, we develop the game theory perspective of IFD for two species that either compete for resources or are in a predator-prey relation. To define stability of an IFD, we use the extension of the ESS concept to two species (Cressman 1992, 2003). Here, we also assume population densities are fixed.

Of course, ecology is also concerned with population dynamics. For habitat selection models, it is usually assumed that IFDs are attained on a much faster timescale than that on which population densities evolve. This allows one to approximate the population dynamics by assuming that species' mean strategies instantaneously track their IFD given current population densities. This is the approach that we carry out at the population timescale level for two-habitat models with either one or two species.

Because we use two different timescales, we use different terms throughout the article to distinguish between them. The corresponding vocabulary is given in table 1.

In this article, we develop a firm theoretical foundation for IFD for two species that either compete for shared resources or are in predator-prey relation, and we integrate this behavioral model with models of population dynamics. In particular, we show that for a single species, IFD is an ESS of a competition game. Then, using a recent extension of ESS for two types of players, we extend single-species IFD for two species by defining it as a two-species ESS. Then, we study population dynamical consequences of the IFD that allow us to determine whether animal behavior, which operates on a short timescale, influences the long-term population dynamics.

Table 1: Terminology

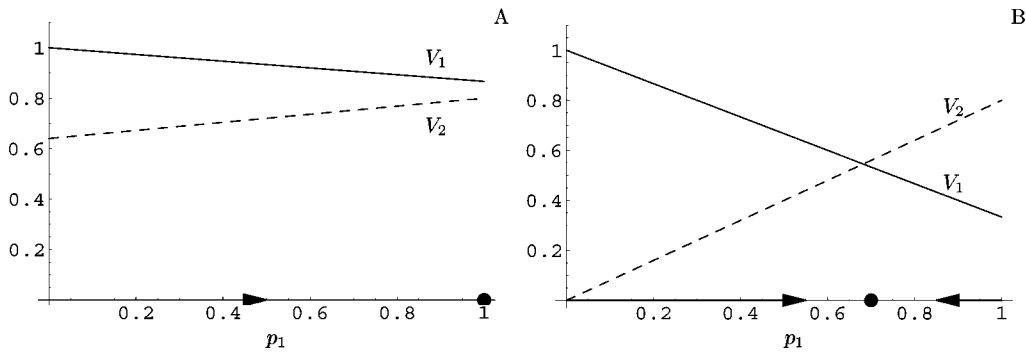| Behavioral timescale	Population timescale
Short-term	Long-term
Fast timescale	Slow timescale
Game dynamics	Population dynamics
Payoff	Fitness
Individual	Population

Figure 1: Ideal free distribution (IFD) for a single species in a two-habitat environment. *A*, Case of low competition ($M = 2$) where all individuals are in the better patch 1 only; *B*, case where competition is more severe ($M = 10$) and, consequently, both patches are occupied. In both cases, the resulting IFD (*filled circle*) is stable with respect to spatial perturbations. Other parameters: $K_1 = 15$, $K_2 = 10$, $r_1 = 1$, $r_2 = 0.8$.

Single-Species Habitat Selection

In this section, we consider a single species that has two possible habitats. The individual fitness depends on the habitat and the species' density in it. Because fitness is often interpreted as reproductive success, we will use the more neutral game-theoretic term of "individual payoff" because the underlying dynamic model is based on individuals adjusting their behavior rather than evolving population densities.

The IFD Is an ESS

Following Křivan and Sirot (2002), we assume that the payoff in habitat i is a linearly decreasing function of population density

$$V_i = r_i\left(1 - \frac{m_i}{K_i}\right), \tag{1}$$

where m_i is the population density in habitat i, r_i is the intrinsic per capita growth rate in habitat i, and K_i is its carrying capacity. The total population size in a two-habitat environment is denoted by M ($= m_1 + m_2$) and the proportion of the population in habitat i is $p_i = m_i/M$. The frequency vector $\mathbf{p} = (p_1, p_2)$, where $p_1 + p_2 = 1$ will be called the population mean strategy.

Let us consider an individual that spends proportion p_1' of its lifetime in habitat 1 and p_2' in habitat 2. Provided population densities are fixed, then its payoff in the population with the population mean strategy $\mathbf{p} = (p_1, p_2)$ is

$$V(\mathbf{p}'; \mathbf{p}) = p_1'V_1(p_1) + (1 - p_1')V_2(p_2).$$

By definition, an IFD is a strategy for which all current choices of an individual as to how to partition its time

between the two habitats have the same payoffs and no other possible choice has a higher payoff. In what follows, we will assume that the per capita intrinsic population growth rate in habitat 1 is higher than that in habitat 2 ($r_1 > r_2$). The following IFD was derived by Křivan and Sirot (2002):

$$p_1 = \begin{cases} 1 & \text{if } M < K_1\dfrac{r_1 - r_2}{r_1} \\[2ex] \dfrac{r_2K_1}{r_2K_1 + r_1K_2} + \dfrac{K_1K_2(r_1 - r_2)}{(r_2K_1 + r_1K_2)M} & \text{otherwise.} \end{cases}$$

$$(2)$$

In the first case, payoff in habitat 1 is higher than the payoff in habitat 2 for all possible population distributions (fig. 1*A*) because the competition in patch 1 is low as a result of low population densities. For higher population abundances, neither of the two habitats is always better than the other, and under the IFD, animal payoff in both habitats must be the same (fig. 1*B*). This implies that $V_1(p_1) = V_2(p_1)$, which leads to the given population distribution.

However, the classical IFD definition does not tackle the problem of stability of the resulting distribution. In fact, the only equilibrium distributions that are biologically meaningful are those that are stable with respect to spatial perturbations. Let us assume that we slightly perturb the IFD. Assume, for example, that there are more animals in habitat 1 than correspond to an IFD (i.e., the perturbed distribution is to the right of the filled circle in fig. 1*B*). Then payoff in habitat 2 (*dashed line*) will be higher than that in habitat 1, and animals start to move to this habitat. Thus, the perturbation will decay in time, and the animal distribution will return to the IFD. A similar argument shows that if there are more animals in habitat 2 than

correspond to the IFD, then again animal distribution will return to the IFD. This verbal argument is denoted in figure 1 by arrows that indicate the direction of animal movement, suggesting there is an implicit dynamic underlying the IFD concept.

The above graphical stability argument based on figure 1 corresponds exactly to the notion of evolutionary stability for a monomorphic population as used in evolutionary game theory (Maynard Smith 1982). Classically, this theory considers two players that directly interact (e.g., the hawk-dove game; Maynard Smith 1982). However, unlike the standard interpretation of this game, we do not assume individuals compete directly with each other in pairwise interactions (for instance, individuals in different habitats cannot compete this way). Instead, we follow the "playing-the-field" approach of Maynard Smith (1982), where individuals "play" against the population mean strategy. In general, a distribution $\mathbf{p}$ is an ESS if there is no other strategy $\mathbf{p}'$ that provides a better payoff in the environment where all individuals use strategy $\mathbf{p}$ (i.e., $\mathbf{p}$ satisfies the NE condition $V(\mathbf{p}'; \mathbf{p}) \leq V(\mathbf{p}; \mathbf{p})$) and this strategy is stable with respect to mutants that provide the same fitness (Maynard Smith 1982)

$$V(\mathbf{p}'; \mathbf{p}') < V(\mathbf{p}; \mathbf{p}') \qquad (3)$$

whenever $V(\mathbf{p}'; \mathbf{p}) = V(\mathbf{p}; \mathbf{p})$ and $\mathbf{p}' \neq \mathbf{p}$. In other words, the second condition in inequality (3) asserts that any alternative best response $\mathbf{p}'$ to the resident strategy $\mathbf{p}$ must do worse against itself than the resident does. In fact, an equivalent definition of an ESS (Hofbauer and Sigmund 1998) ignores the equilibrium condition and asserts that inequality (3) is true only for all strategies $\mathbf{p}'$ close to $\mathbf{p}$. For a single-species, two-habitat game, the strategy given by equation (2) is evolutionarily stable independently of population density. For instance, when $M > K_1(r_1 - r_2)/r_1$,

$$V(\mathbf{p}'; \mathbf{p}') - V(\mathbf{p}; \mathbf{p}') =$$

$$-\frac{\{-K_1K_2r_1 + K_2Mp_1'r_1 + K_1[K_2 + M(p_1' - 1)]r_2\}^2}{K_1K_2M(K_2r_1 + K_1r_2)} < 0.$$

Analogous results also hold for more than two habitats so that the IFD continues to be an ESS. In fact, for single-species habitat selection models, it is not necessary to check inequality (3) because every NE is automatically an ESS. This is a special property of games corresponding to the single-species habitat selection model that does not generalize to two species as we will see later on. In conclusion, we have shown that for the two-habitat, single-species model, the IFD is equivalent to the ESS. In particular, the IFD is stable with respect to spatial perturbations.

IFD Dynamics

So far, we have defined the IFD as a game-theoretical concept that associates to any fixed population density a corresponding species spatial distribution. The IFD assumes that individuals are omniscient and they are completely free to move between patches, but even under these assumptions, it is clear that reaching the IFD is not immediate but takes some time. In fact, it is the trajectories of the actual distributions that are observed in practice because these describe the distribution of individuals between the habitats at a given time. Therefore, it is of interest to describe the time evolution of species distributions. To do this, we need to define strategy dynamics that drive, from any initial species distribution between the two patches, the animal distributions to the corresponding IFD.

The standard game-theoretic dynamics (Maynard Smith 1982) are the replicator dynamics that, for a single species, take the form

$$\frac{dp_i}{dt} = p_i(V_i - \overline{V}), \qquad (4)$$

where p_i is the proportion of the population in habitat i and $\overline{V} (= p_1V_1 + p_2V_2)$ is the mean payoff. This is an unfortunate name in our context because "replicator" has the connotation that change must be based on reproduction. But reproduction is typically not the driving force behind strategy change for habitat selection; rather, it is individuals changing their strategy quickly in response to changes in resource availability in different habitats. One way to interpret equation (4) is to assume that individuals imitate the behavior of others if this observed behavior has a higher payoff. An intuitive way to do this is to switch to these observed higher payoff strategies but only at a rate that increases as the difference in one's own current payoff and the observed payoff increases. Schlag (1997) showed that such learning rules lead to replicator-like dynamics that increase the proportion of individuals in all habitats whose payoff is better than average (and at a rate that increases as this difference increases).

In the case of two habitats and the payoff function given by equation (1), the replicator dynamics are

$$\frac{dp_1}{dt} = p_1(1 - p_1)(V_1 - V_2). \qquad (5)$$

It is easy to see that the IFD given by equation (2) is a globally asymptotically stable equilibrium for the replicator dynamics.

The IFD for Two Competing Species in a Two-Habitat Environment

In this section, we develop the theory of IFD for two species that compete in each of the two habitats. We take the following Lotka-Volterra-type individual payoff functions in each habitat:

$$V_i(\mathbf{p}, \mathbf{q}; M, N) = r_i\left(1 - \frac{p_i M}{K_i} - \frac{\alpha_i q_i N}{K_i}\right) \quad i = 1, 2,$$

$$W_j(\mathbf{p}, \mathbf{q}; M, N) = s_j\left(1 - \frac{q_j N}{L_j} - \frac{\beta_j p_j M}{L_j}\right) \quad j = 1, 2. \quad (6)$$

Here, M and N are the total population sizes of species 1 and 2, respectively; vector $\mathbf{p} = (p_1, p_2)$ denotes the proportion of the first population in habitat 1 (p_1) and in habitat 2 (p_2); vector $\mathbf{q} = (q_1, q_2)$ denotes the distribution of the second population; r_i and K_i are the intrinsic growth rate and carrying capacity, respectively, for species 1 in habitat i; and s_j and L_j are the intrinsic growth rate and carrying capacity, respectively, for species 2 in habitat j. Also, α_i and β_i are interspecific competition coefficients in habitat i that model the effect of the second species on the first species and of the first species on the second species, respectively. (We sometimes abuse notation slightly by referring to species 1 and 2 as species M and N, respectively.) We remark that the model in equation (6) extends the one considered by Křivan and Sirot (2002) because in that article, the competition coefficients were habitat independent (i.e., $\alpha_1 = \alpha_2 = \alpha$ and $\beta_1 = \beta_2 = \beta$). Here, we relax this assumption, and we will show later that this substantially affects the dynamics at the population timescale level.

Payoffs of invaders with individual strategies $\mathbf{p}' = (p_1', p_2')$ and $\mathbf{q}' = (q_1', q_2')$ when the monomorphic populations have strategies $\mathbf{p} = (p_1, p_2)$ and $\mathbf{q} = (q_1, q_2)$ are

$$V(\mathbf{p}'; \mathbf{p}, \mathbf{q}) = p_1' V_1(\mathbf{p}, \mathbf{q}) + p_2' V_2(\mathbf{p}, \mathbf{q}),$$

$$W(\mathbf{q}'; \mathbf{p}, \mathbf{q}) = q_1' W_1(\mathbf{p}, \mathbf{q}) + q_2' W_2(\mathbf{p}, \mathbf{q}).$$

Following single-species cases, we define the IFD for two species as an ESS of the underlying game. Thus, we seek an equilibrium pair of distributions $\mathbf{p} = (p_1, p_2)$ and $\mathbf{q} = (q_1, q_2)$ ($0 \le p_i, q_i \le 1$) that is stable with respect to spatial perturbations at fixed population densities M and N. The following two-species NE condition is straightforward, namely,

$$V(\mathbf{p}'; \mathbf{p}, \mathbf{q}) \le V(\mathbf{p}; \mathbf{p}, \mathbf{q}),$$

$$W(\mathbf{q}'; \mathbf{p}, \mathbf{q}) \le W(\mathbf{q}; \mathbf{p}, \mathbf{q}), \quad (7)$$

for all possible strategies $\mathbf{p}' = (p_1', p_2')$ and $\mathbf{q}' = (q_1', q_2')$. However, the extension of the single-species stability in inequality (3) to multiple species is nontrivial because several possibilities have been considered over the years. As we will see, the game-theoretic "two-species ESS" condition taken from Cressman (1992; see also Cressman 2003; Garay et al. 2003) is the one that corresponds to stability with respect to spatial perturbations in our habitat selection model. This is a strategy pair such that at least one of the inequalities

$$V(\mathbf{p}'; \mathbf{p}', \mathbf{q}') < V(\mathbf{p}; \mathbf{p}', \mathbf{q}'),$$

$$W(\mathbf{q}'; \mathbf{p}', \mathbf{q}') < W(\mathbf{q}; \mathbf{p}', \mathbf{q}') \quad (8)$$

is true for each perturbed distribution $\mathbf{p}' = (p_1', p_2')$ and $\mathbf{q}' = (q_1', q_2')$ that is sufficiently close (but not equal) to $(\mathbf{p}, \mathbf{q})$.

Thus, we rule out the original suggestion of Taylor (1979; see also Thomas 1986), who considers the sum of the two payoff functions, V and W, and searches for a single-species ESS with respect to this lumped payoff function. This suggestion is not acceptable because it assumes that the two species "share" their payoff. To rephrase inequality (8), a two-species ESS is then one where, for all other nearby population mean distributions, at least one species does better playing its ESS strategy than playing the mean strategy of this species. For the predator-prey two-habitat model, we will also need the concept of an (interior) weak two-species ESS, that is, a pair $(\mathbf{p}, \mathbf{q})$ that satisfies inequality (8) whenever $\mathbf{p}' \ne \mathbf{p}$, $\mathbf{q}' \ne \mathbf{q}$, and $(\mathbf{p}', \mathbf{q}')$ is close to $(\mathbf{p}, \mathbf{q})$.

Two-species ESSs for two-habitat games have not previously been analyzed in the literature. They can be determined graphically by plotting, for a given species, the line in the unit square where both its pure strategies have the same payoff (fig. 2). These two "equal-payoff" lines are the solutions to

$$V_1(\mathbf{p}, \mathbf{q}) = V_2(\mathbf{p}, \mathbf{q}),$$

$$W_1(\mathbf{p}, \mathbf{q}) = W_2(\mathbf{p}, \mathbf{q}) \quad (9)$$

for species 1 (*solid line*) and 2 (*dashed line*), respectively. The six diagrams in figure 2 are representative of the possible qualitative situations (for a complete set of qualitative diagrams, see fig. 2 and app. A in Křivan and Sirot 2002). By using $p_2 = 1 - p_1$ and $q_2 = 1 - q_1$, the equal-payoff line for species 1 is
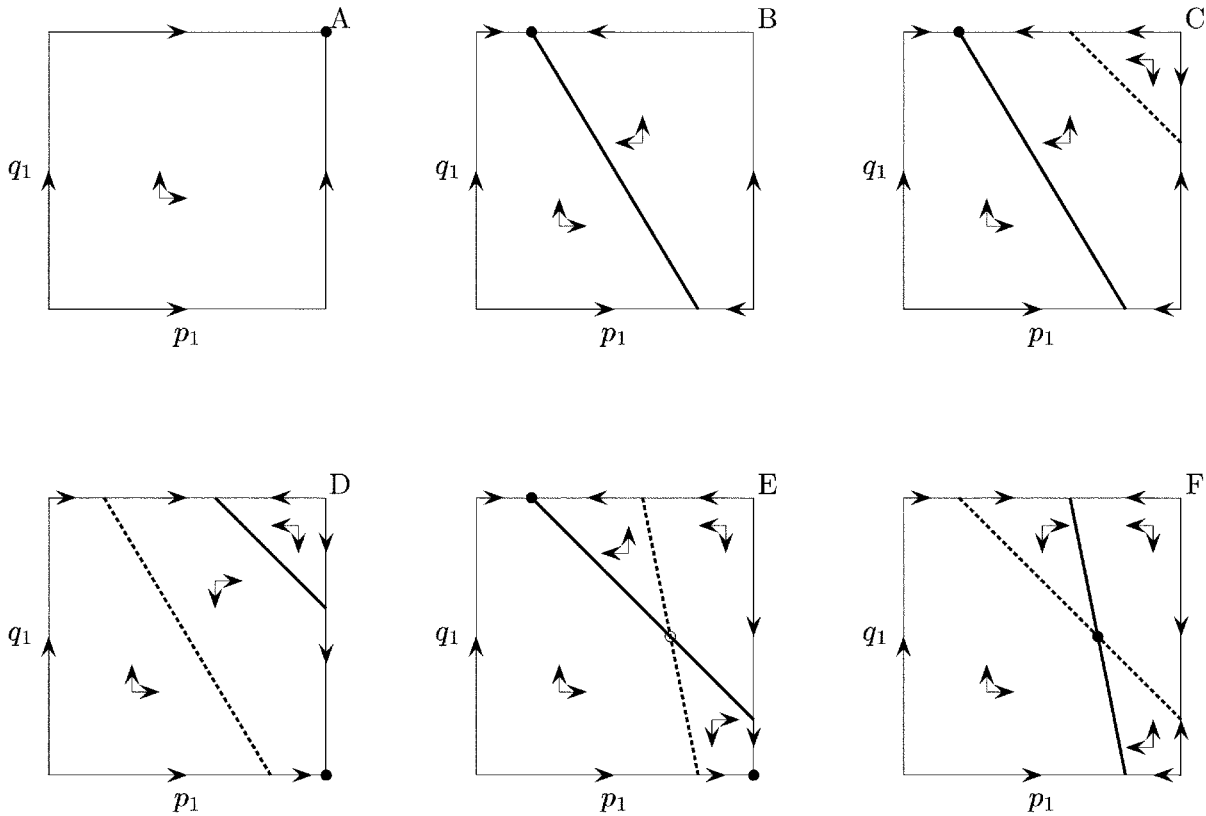
Figure 2: Ideal free distribution for two competing species (*filled circles*) at fixed population densities; unstable Nash equilibrium = *open circle*

$$q_1 = \frac{K_1[K_2(r_1 - r_2) + r_2(M + N\alpha_2)]}{N(K_2 r_1 \alpha_1 + K_1 r_2 \alpha_2)}$$

$$- \frac{M(K_2 r_1 + K_1 r_2)}{N(K_2 r_1 \alpha_1 + K_1 r_2 \alpha_2)} p_1$$

and for species 2 is

$$q_1 = \frac{L_1[L_2(s_1 - s_2) + s_2(N + M\beta_2)]}{N(L_2 s_1 + L_1 s_2)}$$

$$- \frac{M(L_2 s_1 \beta_1 + L_1 s_2 \beta_2)}{N(L_2 s_1 + L_1 s_2)} p_1.$$

Clearly, both of these lines have negative slopes that we assume intersect at a point that is not on the boundary of the unit square. If these lines intersect in the interior of the unit square, then this strategy pair automatically satisfies the NE condition given by inequality (7).

An ESS (fig. 2, *filled circles*) on the boundary of the unit square can then be found by following the arrows in figure 2 that indicate directions in which the payoff for species 1 increases (*horizontal arrows*) and similarly for species 2

(*vertical arrows*). A boundary ESS is then any point where all nearby boundary arrows point toward it as well as all nearby interior arrows perpendicular to this boundary. In particular, a vertex is an ESS if and only if both adjacent boundary arrows point in that direction. That is, if the two equal-payoff lines do not intersect in the unit square (fig. 2*A*–2*D*), then there exists a unique ESS such that at least one population occupies one habitat only. To determine whether an interior intersection of the two equal-payoff lines is a two-species ESS requires more care. The analysis of figure 2*E* shows the interior intersection (*empty circle*) is not a two-species ESS even though it satisfies inequality (7). However, if the two equal-payoff lines are interchanged (fig. 2*F*), the interior intersection is the only two-species ESS.

To summarize, for the two-species, two-habitat competition model, there is exactly one ESS for all possible parameter values except as in figure 2*E*, where the two equal-payoff lines intersect in the interior of the unit square and the equal-payoff line for species 2 is steeper than the equal-fitness line for species 1, which happens when
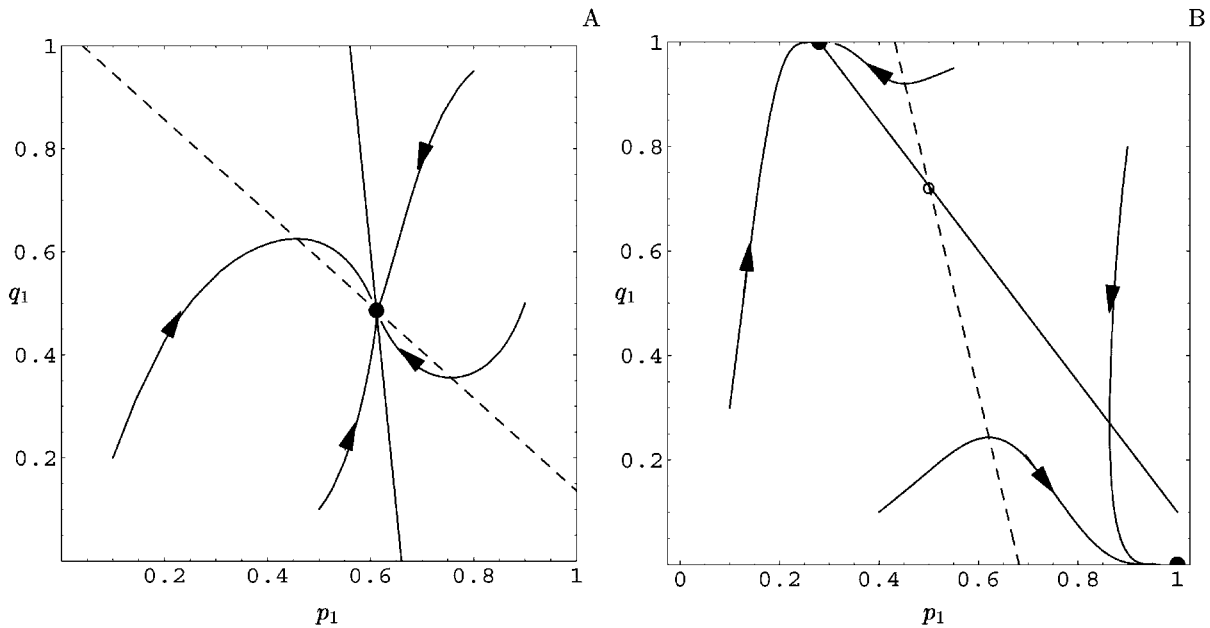
Figure 3: Time evolution of two-species distributions governed by replicator game dynamics show convergence to the ideal free distribution (IFD). A ($\alpha_1 = 0.1$, $\alpha_2 = 0.1$, $\beta_1 = 0.9$, $\beta_2 = 0.9$), Case where there is an interior IFD (cf. fig. 2F). B ($\alpha_1 = 0.8$, $\alpha_2 = 0.8$, $\beta_1 = 4$, $\beta_2 = 4$), Unstable interior Nash equilibrium (cf. fig. 2E). Other parameters: $K_1 = 15$, $K_2 = 10$, $L_1 = 12$, $L_2 = 10$, $r_1 = 1$, $r_2 = 1$, $s_1 = 1$, $s_2 = 1$, $M = 3$, $N = 3$.

$$\frac{r_1 K_2 + r_2 K_1}{\alpha_1 r_1 K_2 + \alpha_2 r_2 K_1} > \frac{\beta_1 s_1 L_2 + \beta_2 s_2 L_1}{s_1 L_2 + s_2 L_1}.$$

In this case, there are two ESSs, and without some additional information (e.g., about the order of colonization), it is impossible to predict which of the two corresponding species spatial distributions will be attained for the two species. This inequality can be rewritten as

$$r_1 s_1 K_2 L_2 (1 - \alpha_1 \beta_1) + r_1 s_2 K_2 L_1 (1 - \alpha_1 \beta_2)$$
$$+ r_2 s_1 K_1 L_2 (1 - \alpha_2 \beta_1) + r_2 s_2 K_1 L_1 (1 - \alpha_2 \beta_2) < 0, \quad (10)$$

a form that is more convenient for certain observations. For instance, if interspecific competition is weak (α_i and β_j are sufficiently small so that $\alpha_i \beta_j < 1$), a unique ESS exists. The same holds if one species is dominant over the other species in both habitats (e.g., α's are much smaller than β's or vice versa).

The replicator equation (Taylor 1979) for the two competing species is given by

$$\frac{dp_1}{dt} = p_1(1 - p_1)(V_1(\mathbf{p}, \mathbf{q}) - V_2(\mathbf{p}, \mathbf{q})),$$

$$\frac{dq_1}{dt} = q_1(1 - q_1)(W_1(\mathbf{p}, \mathbf{q}) - W_2(\mathbf{p}, \mathbf{q})). \quad (11)$$

A phase plane analysis of the six representative cases in figure 2 shows that a two-species ESS corresponds to a locally asymptotically stable equilibrium of the replicator equation. This is clearly shown in figure 3. In figure 3A, the interior equilibrium is the ESS, and species distribution converges to this IFD corresponding to figure 2F, whereas figure 3B shows distributions that converge to the two alternative IFDs when the intersection of the two equal-fitness lines is not an ESS (i.e., corresponding to fig. 2E).

The IFD for Predator-Prey Species in Two-Habitat Environment

Now we consider a predator-prey model in a two-habitat environment. We assume that both prey and predators are mobile and they move between patches so that their payoff maximizes. We will assume Lotka-Volterra-type fitness functions

$$V_i(\mathbf{p}, \mathbf{q}; M, N) = r_i\left(1 - \frac{\sigma p_i M}{K_i} - \alpha_i q_i N\right),$$

$$W_j(\mathbf{p}, \mathbf{q}; M, N) = s_j(-1 + \beta_j p_j M). \quad (12)$$

Here, V_i is the payoff of prey, and W_i is the payoff of predators in habitat i ($i = 1, 2$). The case where there is

no intraspecific competition ($\sigma = 0$) was studied by Křivan (1997) and Křivan and Schmitz (2003).

To determine the IFD, we will assume without loss of generality that the predator's intrinsic death rates satisfy $s_1 > s_2$. The equal-payoff line for the predator ($W_1(\mathbf{p}, \mathbf{q}; M, N) = W_2(\mathbf{p}, \mathbf{q}; M, N)$) is

$$p_1 = \frac{s_1 - s_2 + s_2\beta_2 M}{M(s_1\beta_1 + s_2\beta_2)},$$

which is a vertical line (fig. 4, *dashed line*). If this line is to the right of the unit square (i.e., when expression for p_1 is larger than 1), then all predators must occupy habitat 2 only ($q_1 = 0$), and the problem reduces to a single-species habitat selection (for the prey), which we know has a unique ESS and thus IFD. For example, this happens when density of prey is low, so predators cannot balance their higher mortality rate in habitat 1 by higher foraging in that habitat, and, consequently, the best strategy for them is to spend all their time in the habitat with the lower mortality rate (i.e., habitat 2 in our case).

The equal-payoff line for prey

$$q_1 = \frac{K_2 r_1 - K_2 r_2 + K_2 N r_2 \alpha_2 + M r_2 \sigma}{K_2 N r_1 \alpha_1 + K_2 N r_2 \alpha_2}$$
$$- \frac{(K_2 r_1 + K_1 r_2)M\sigma}{(r_1\alpha_1 + r_2\alpha_2)K_1 K_2 N}p_1$$

is shown as the solid line in figure 4. This line is either decreasing (for $\sigma > 0$; fig. 4B) or horizontal (for $\sigma = 0$; fig. 4A). Following Křivan (1997), it can be shown that if one of the two lines does not intersect the unit square, there exists (generically) a unique ESS on the boundary of the square. Finally, if the two equal-payoff lines intersect in the interior of the unit square, this point is the only strategy pair that satisfies the NE condition given by inequality (7). It is also a weak two-species ESS (see fig. 4) for both cases (i.e., $\sigma > 0$ and $\sigma = 0$).

In the same way that there is a correspondence between IFD and stable equilibrium of replicator dynamics for the competition case, there is a similar correspondence for the predator-prey interactions. The replicator dynamics in equation (11) for the predator-prey game become

$$\frac{dp_1}{dt} = p_1(1 - p_1)$$
$$\times \left[r_1 - r_2 - \sigma M\left(\frac{r_1 p_1}{K_1} - \frac{r_2 p_2}{K_2}\right) - N(r_1\alpha_1 q_1 - r_2\alpha_2 q_2)\right],$$
$$\frac{dq_1}{dt} = q_1(1 - q_1)[-(s_1 - s_2) + M(s_1 p_1 \beta_1 - s_2 p_2 \beta_2)].$$
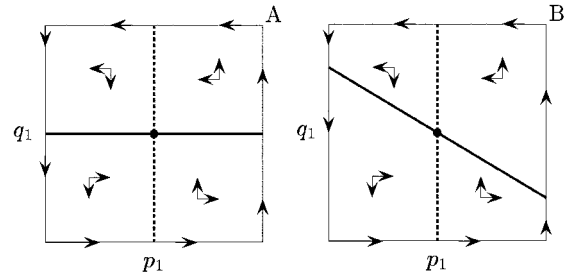$$(13)$$

Figure 4: Ideal free distribution (*filled circle*) for the predator-prey game. *A*, No intraspecific competition among prey ($\sigma = 0$); *B*, competition among prey ($\sigma > 0$).

Then, the weak two-species ESS is an equilibrium of the above replicator dynamics, and it is stable with respect to equation (13) but may not be locally asymptotically stable. This is clearly shown in figure 5A, where there is no intraspecific prey competition, while it is globally asymptotically stable under positive competition (fig. 5B).

Ecological Timescale

As discussed in the introduction to this article, individuals facing habitat selection, either in the field or in experiments, typically change their strategy rapidly (relative to their generational time) in response to changing environments. This suggests that the timescale for population dynamics is much longer than that of the population distribution evolution. In this section, we consider the population dynamics for the previous models under the assumption that mean strategies are instantaneously at their IFD for the current density, and we ask whether the short-term behavior influences long-term population dynamics.

The Single-Species Model

The IFD (such as the one for a single species given by eq. [2]) depends naturally on the overall population density (M), and in what follows we will make this dependency explicit by writing $\mathbf{p}(M)$ and so forth. Now individual payoffs do translate into population fitness. Specifically, the expected fitness of the population mean strategy (that is assumed to be distributed according to the IFD) is

$$F(M) = p_1(M)V_1(\mathbf{p}(M), M) + p_2(M)V_2(\mathbf{p}(M), M)$$
$$= p_1(M)\left(1 - \frac{p_1(M)M}{K_1}\right) + p_2(M)\left(1 - \frac{p_2(M)M}{K_2}\right).$$

If generation time is λ, the continuous-time population dynamic becomes
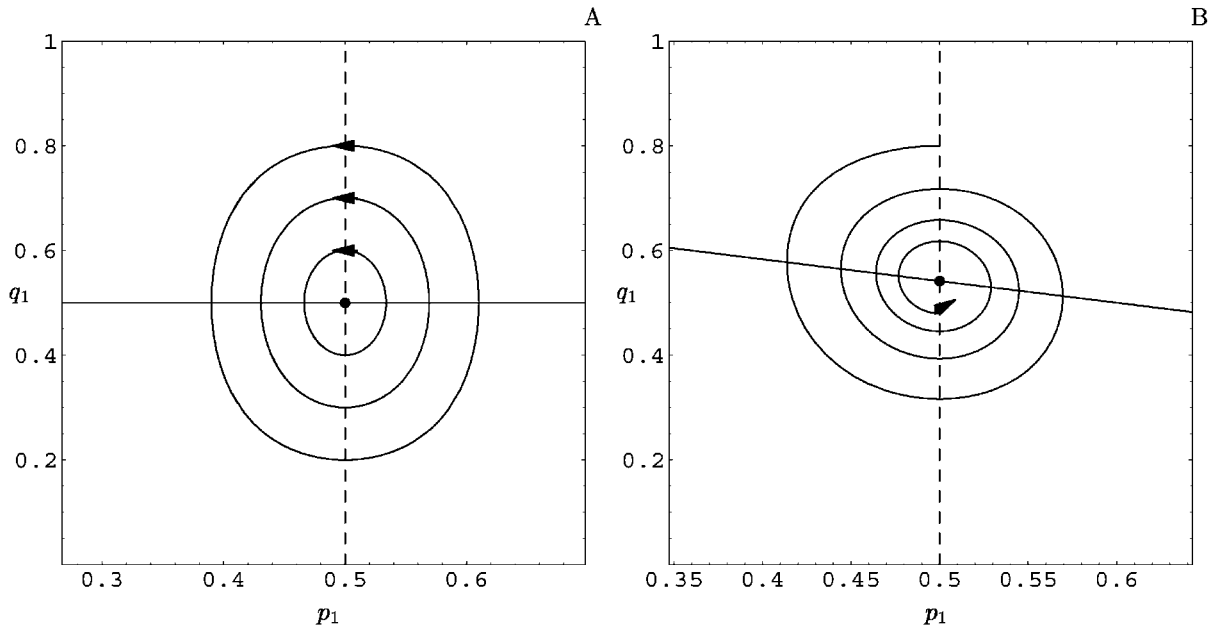
Figure 5: Trajectories of the replicator dynamics of predator-prey distribution after perturbation from the ideal free distribution. *A*, Case where there is no intraspecific competition among prey ($\sigma = 0$); *B*, Prey-intraspecific competition ($\sigma = 0.5$). Other parameters: $\alpha_1 = 0.1$, $\alpha_2 = 0.1$, $\beta_1 = 0.9$, $\beta_2 = 0.9$, $K_1 = 15$, $K_2 = 10$, $r_1 = 1$, $r_2 = 1$, $s_1 = 1$, $s_2 = 1$.

$$\frac{dM(t)}{dt} = \frac{1}{\lambda} M(t) F(M(t)), \tag{14}$$

which is given by Křivan and Sirot (2002) in explicit expanded form. Because trajectories of this one-dimensional dynamic depend only on λ up to a change in timescale, any choice of positive λ, such as $\lambda = 1$, will not affect the following discussion of the long-term outcome of these dynamics and their stability properties.

We first show that at the population equilibrium, all patches will be completely occupied. This is a nontrivial prediction because outside of the population equilibrium, consumers, when at low densities, will occupy the better patch only (see eq. [2]). Suppose M^* is a positive population equilibrium of equation (14). Then, all strategies that are present in the IFD (i.e., those strategies for which $p_i(M^*) > 0$) must satisfy

$$V_i(\mathbf{p}(M^*), M^*) = 0$$

because all these $V_i(\mathbf{p}(M^*), M^*)$ are equal at the IFD (animal fitness is equalized over all occupied patches under the IFD) and the equilibrium population growth rate is 0 ($F(M^*) = 0$). Moreover, in population equilibrium, all habitats will be occupied because if some habitat were empty (i.e., $p_i(M^*) = 0$), then $V_i(\mathbf{p}(M^*), M^*) = r_i > 0$, so individuals moving to that habitat would obtain a higher

payoff than those staying in other habitats. Thus, at the population equilibrium M^*, all habitats will be occupied, and individual fitness will be the same (and equal to 0) in all habitats. This immediately implies that at the population equilibrium, the density in each habitat is given by its carrying capacity (i.e., $m_i^* = K_i$ for all i), and so, when there are only two habitats, the overall population abundance is $M^* = K_1 + K_2$.

It is interesting to point out that the same qualitative result emerges from the alternative model for population dynamics that assumes that animals do not move between habitats (e.g., sessile organisms). This leads to the logistic equation

$$\frac{dm_i}{dt} = m_i \left(1 - \frac{m_i}{K_i}\right)$$

in each habitat ($i = 1, 2$). Contrary to the case where animal distribution follows IFD, now the timescale for the dynamics of animal distribution (given by $p_i = m_i/M$) is of the same order as the population dynamics. Clearly, m_i converges to $m_i^* = K_i$ for all i and $M^* = K_1 + K_2$. That is, from a population point of view that does not observe whether individuals change habitats, the two stable limiting distributions look identical; namely, the proportion of individuals in a given habitat is exactly equal to its

carrying capacity. Thus, one can wonder whether this is a general property or whether this is limited to the special case of single-species habitat selection models. In fact, we will already see that individual behavior is important for two-species IFD (i.e., qualitative predictions when animals can move are different from those when they cannot).

The Two-Species Competition Model

Here, we consider population dynamics of two competing species in a two-habitat environment. We compare two types of population dynamics. The first type assumes that animals do not move between habitats at all, while the second type of population dynamics assumes that at each time, the distribution of animals follows the two-species IFD. These two cases can describe differences in population dynamics of competing sessile organisms versus those that are highly mobile.

First, let us assume that individuals do not move between habitats. This leads to an elementary analysis of the population dynamics because the two-species dynamics in habitat 1 are completely independent of those of habitat 2. Thus, the dynamics in habitat i form the following standard two-species competition model of Lotka-Volterra type:

$$\frac{dm_i}{dt} = m_i r_i \left(1 - \frac{m_i}{K_i} - \frac{\alpha_i n_i}{K_i}\right) \quad i = 1, 2,$$

$$\frac{dn_j}{dt} = n_j s_j \left(1 - \frac{n_j}{L_j} - \frac{\beta_j m_j}{L_j}\right) \quad j = 1, 2. \quad (15)$$

Suppose each habitat has an equilibrium where both species coexist. The corresponding equilibrium is given by

$$m_i^* = \frac{K_i - \alpha_i L_i}{1 - \alpha_i \beta_i},$$

$$n_i^* = \frac{L_i - \beta_i K_i}{1 - \alpha_i \beta_i} \quad i = 1, 2.$$

Second, let us consider mobile animals whose spatial distributions $\mathbf{p}(M, N)$ and $\mathbf{q}(M, N)$ of species 1 and 2, respectively, track the IFD. Population dynamics for overall species densities M and N are then given by the following model:

$$\frac{dM}{dt} = M[p_1 V_1(\mathbf{p}, \mathbf{q}; M, N) + p_2 V_2(\mathbf{p}, \mathbf{q}; M, N)],$$

$$\frac{dN}{dt} = N[q_1 W_1(\mathbf{p}, \mathbf{q}; M, N) + q_2 W_2(\mathbf{p}, \mathbf{q}; M, N)]. \quad (16)$$

Substituting $M^* = m_1^* + m_2^*$, $N^* = n_1^* + n_2^*$, $p_i^* = m_i^*/M^*$, and $q_i^* = n_i^*/N^*$ in equation (16) shows that the interior equilibrium of equation (15) where animals do not move between patches is also an equilibrium of equation (16) when animals move and their distribution corresponds to the IFD. The interesting question now is how the stability of the model without migration (eq. [15]) compares to the model where animals migrate (eq. [16]). We know that the model without migration is globally asymptotically stable in both habitats if and only if $1 - \alpha_1 \beta_1 > 0$ and $1 - \alpha_2 \beta_2 > 0$. However, there is no relation between these inequalities and inequality (10) that determines whether distribution $(\mathbf{p}^*, \mathbf{q}^*)$ is IFD for the population equilibrium densities M^* and N^* when animals do migrate.

Thus, it is easy to construct examples that show that a stable population equilibrium exists for the model without migration (eq. [15]) under which the species distribution is not stable with respect to small spatial perturbations; that is, it does not correspond to the IFD (fig. 6). Figure 6 (*left column*) shows the case where animals do not move between habitats and the corresponding animal distribution is $p_1^* = 10/11$ and $q_1^* = 1/11$ at the globally asymptotically stable population equilibrium $M^* = N^* = 11$ of equation (15). However, for the model that assumes migration (fig. 6, *right column*), this spatial distribution (fig. 6, *bottom right panel*, *open circle*) is not stable with respect to small spatial perturbations (because inequality [10] holds; cf. fig. 6, *bottom right panel*, with fig. 2*E*). Thus, this spatial animal distribution is not an IFD for the model where animals move between habitats. Small perturbations of spatial distributions of both populations that are at the population equilibrium lead (on a fast behavioral timescale) to spatial redistribution and to a new population equilibrium as shown in figure 6 (*top right panel*). Here, animal movement between habitats leads to complete segregation of the two species as shown in figure 6 (*bottom right panel*); that is, either species M occupies habitat 1 while species N occupies habitat 2 or species M occupies habitat 2 while species N occupies habitat 1, and species equilibrial densities are given by the corresponding carrying capacities ($M^* = N^* = 19$ and $M^* = N^* = 2$, respectively). To rephrase the analysis of this example, we find that individual animal behavior can have an important effect on the population dynamics. When animals cannot move between habitats, both species coexist in each habitat. However, if animals migrate, the species can seg-
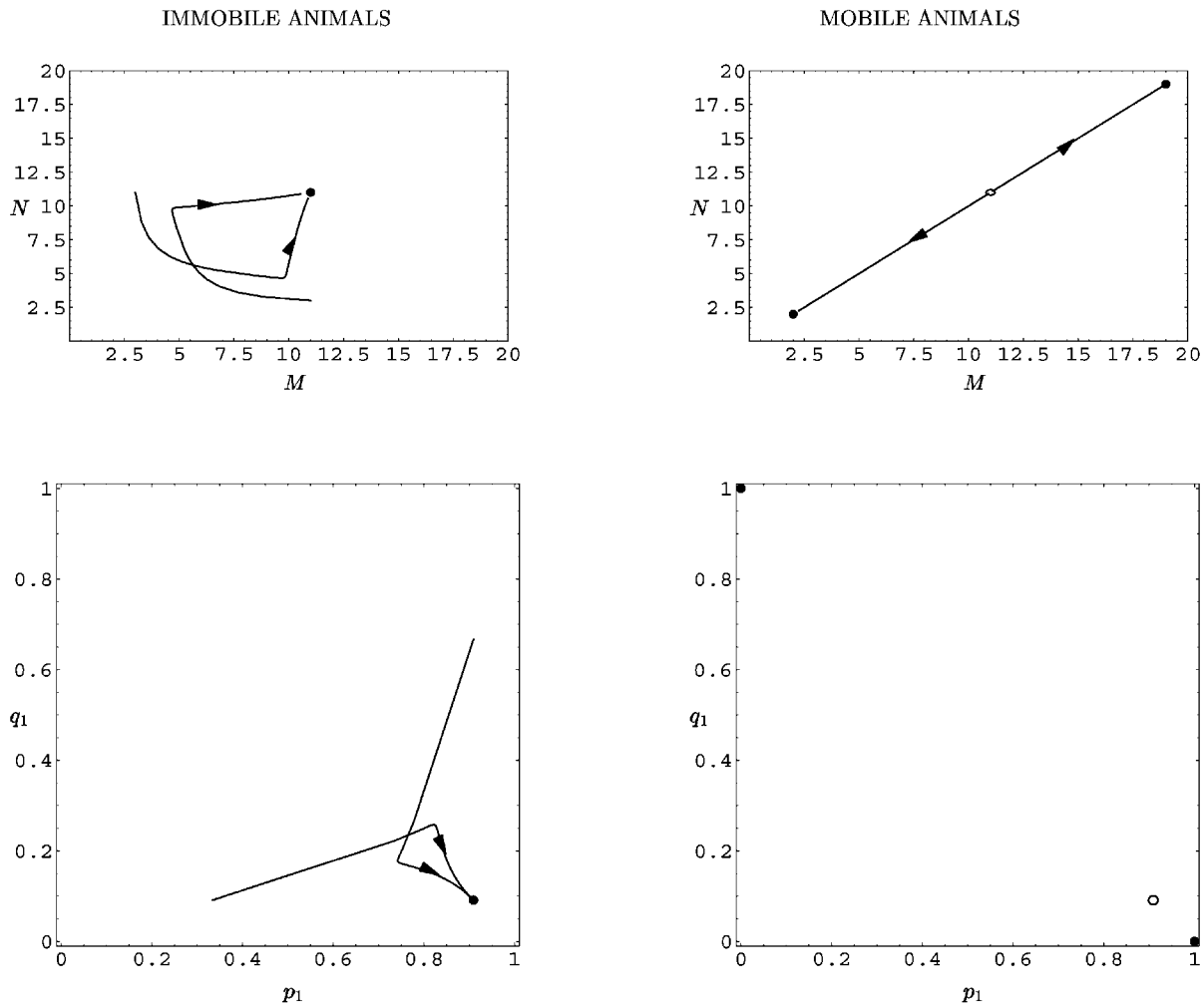
IMMOBILE ANIMALS   MOBILE ANIMALS

Figure 6: *Top*, Overall population dynamics of two competing species *M* and *N* in the species density phase space. Two trajectories are shown. *Bottom*, Corresponding species distributions over two habitats. *Left*, Individuals do not move between habitats. *Right*, Individuals are mobile and follow the ideal free distribution (IFD). *Bottom right*, No nonconstant trajectories because the two species immediately segregate into separate habitats (i.e., there are two possible IFDs: $p_1 = 1$, $q_1 = 0$ and $p_1 = 0$, $q_1 = 1$; *filled circles*) and stay segregated as their population sizes approach equilibrium. The distribution that corresponds to $p_1 = 10/11$ and $q_1 = 1/11$ at the population equilibrium for immobile animals (*bottom right, open circle*) is not an IFD, and this population equilibrium (*top right, open circle*) is destabilized by animal movement. Parameters: $\alpha_1 = 9$, $\alpha_2 = 0.1$, $\beta_1 = 0.1$, $\beta_2 = 9$, $K_1 = 19$, $K_2 = 2$, $L_1 = 2$, $L_2 = 19$, $r_1 = 1$, $r_2 = 0.1$, $s_1 = 0.1$, $s_2 = 1$.

regate in separate habitats. That is, in this latter case, segregation is maintained by the potential of interspecific competition, giving a concrete interpretation of the "ghost of competition" as discussed by Morris (1999).

Conversely, figure 7 shows that population dynamics also have an important effect on animal behavior because a population equilibrium can be unstable at the corresponding IFD when animals migrate. In this figure, there exists an unstable population equilibrium for equation (16) with migration (fig. 7, *upper panel, open circle*) for which the corresponding species distribution is an IFD

(i.e., stable with respect to spatial perturbations in species distribution because inequality [10] does not hold). This equilibrium is shown in the bottom panel as the filled circle (which emphasizes the fact that this spatial distribution is an IFD, i.e., stable) inside the square. However, the corresponding population equilibrium is unstable, which means that small perturbations to population densities lead to a departure from this equilibrium and to a new population equilibrium (as documented by two trajectories shown in fig. 7, *upper panel*). Because the spatial distributions change as population densities change, the
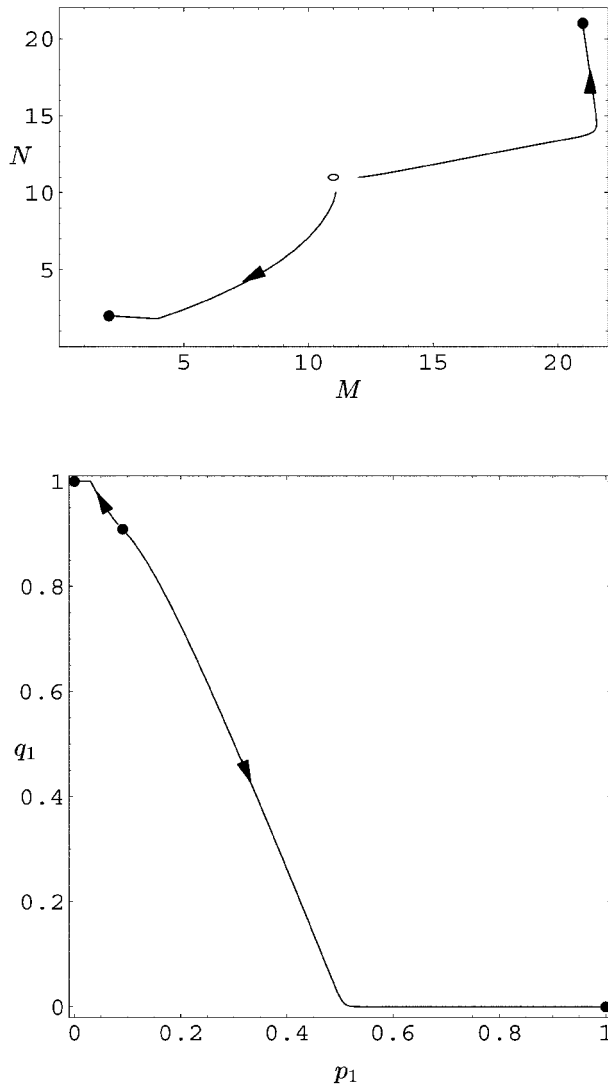
Figure 7: Interior ideal free distribution (*bottom, interior filled circle*) and the corresponding population equilibrium, which is unstable (*top, open circle*). Perturbations in population densities lead to departure from this population equilibrium and to convergence to a new population equilibrium and new species distribution. Two such trajectories are shown. Parameters: $\alpha_1 = 0.1$, $\alpha_2 = 11$, $\beta_1 = 11$, $\beta_2 = 0.1$, $K_1 = 2$, $K_2 = 21$, $L_1 = 21$, $L_2 = 2$, $r_1 = 1$, $r_2 = 0.1$, $s_1 = 0.1$, $s_2 = 1$.

species spatial distribution changes too, and a new IFD (fig. 7, filled circles on the boundary of the square) is reached at the new population equilibrium.

The examples for figures 6 and 7 show that several forces can support the evolution of segregation into two different habitats in two-species models. Specifically, in figure 6, mobile animals may segregate even though the population dynamics suggest that species will coexist. In figure 7, it

is the population dynamics that underlie habitat segregation and not individual behavior. Thus, under these latter conditions, there will be no long-term difference in population densities and population spatial distributions whether individuals are mobile.

On the other hand, when interaction coefficients are independent of habitat (i.e., when $\alpha_1 = \alpha_2 = \alpha$ and $\beta_1 = \beta_2 = \beta$), we do see that equation (15) is (globally) asymptotically stable if and only if $(\mathbf{p}^*, \mathbf{q}^*)$ is an IFD at fixed population densities M^* and N^*. Furthermore, in this case, both of these conditions are equivalent to the asymptotic stability of $(\mathbf{p}^*, \mathbf{q}^*; M^*, N^*)$ in equation (16) (the technical proof based on the linearization technique is given in app. A).

The Two-Species Predator-Prey Model

Here we consider population dynamics for the predator-prey model at the ecological timescale level. First, let us assume that individuals do not move between habitats. This again leads to an elementary analysis of the population dynamics because the two-species dynamics in habitat 1 are completely independent of those in habitat 2. Thus, the dynamics in habitat i now form the following standard two-species predator-prey model of Lotka-Volterra type:

$$\frac{dm_i}{dt} = m_i r_i \left(1 - \frac{\sigma m_i}{K_i} - \alpha_i n_i\right) \quad i = 1, 2,$$

$$\frac{dn_j}{dt} = n_j s_j (-1 + \beta_j m_j) \quad j = 1, 2. \tag{17}$$

If there is an equilibrium where both species coexist in each habitat, it is given by

$$m_i^* = \frac{1}{\beta_i},$$

$$n_i^* = \frac{1 - \sigma/(\beta_i K_i)}{\alpha_i} \quad i = 1, 2.$$

This equilibrium is globally asymptotically stable provided $\sigma > 0$ and neutrally stable if $\sigma = 0$.

Second, let us consider the case where animals can move between the two patches and their spatial distribution $\mathbf{p}(M, N)$ and $\mathbf{q}(M, N)$ of species 1 and 2, respectively, track the IFD. Then, population dynamics are given by equation (16), where we substitute the corresponding fitness functions from equation (12). Appendix B shows that for positive levels of intraspecific competition ($\sigma > 0$), a population equilibrium where predator and prey coexist in each

habitat is always asymptotically stable for mobile animals just as it is for immobile animals as noted above. That is, for predator-prey interactions, an IFD at population equilibrium is stable for population dynamics based on either mobile or immobile animals. Thus, in this case, animal behavior does not influence the qualitative predictions of population dynamics.

Discussion

The IFD is a key component of evolutionary ecology that aims to understand species distribution in habitats where resources are patchily distributed. Fretwell and Lucas (1970) defined the IFD for a single species in a habitat consisting of two or more resource patches. They assumed that animals move freely and instantaneously between patches and settle in the patch with the highest suitability. In our terminology, the suitability of a patch determines the individual's payoff at the behavioral timescale level and its fitness at the population timescale level (see table 1). Thus, under the IFD, all individuals will have the same fitness. In this setting, the individual strategy is the proportion of the lifetime an average animal will spend in either patch. Moreover, because this fitness also depends on the strategy of other individuals, the IFD is a game-theoretical concept.

One of the key concepts used in evolutionary ecology is the notion of ESS (Maynard Smith 1982). In fact, the IFD is often referred to in the literature as an example of an ESS. By definition, an ESS is the best strategy when played against itself, and it is stable with respect to other invading strategies that when played against it give the same fitness. The first condition implies that in our setting, fitness of all individuals is the same. Thus, the original definition of the IFD coincides with the first part of the ESS definition for a single species. How about the second stability condition? A natural stability requirement for the IFD in this setting is stability with respect to perturbations in species distribution. In other words, we require that after the species distribution is perturbed, then it moves back toward the original IFD distribution. Distributions that are unstable with respect to small perturbations cannot persist in nature. In this article, we showed that IFD stability is equivalent to ESS stability for a single species at fixed population density. That is, a resident population that resists invasion by a few individuals by using a different strategy (i.e., an ESS in the classical sense of Maynard Smith [1982]) is also an IFD distribution in that it is stable with respect to spatial perturbations (and conversely). Then, we went further and extended the IFD for two species (that are either competing for spatially distributed resources or are in a predator-prey interaction in two spatially separated patches) by defining it as a two-species ESS (Cressman 2003).

In the literature, there have been several other attempts to extend the IFD for single species to multispecies environments, assuming fixed population densities. Some of these studies assumed that the equal payoff lines for the two species do not intersect (Possingham 1992; Grand 2002), which was due to the particular choice of payoff functions. Under such an assumption, each species occupies one habitat only, and coexistence of both species in one habitat is impossible. Graphically, the IFD for two competing species can be visualized in the species density phase space by isoclines (Rosenzweig 1979, 1981, 1986, 1991) or by isodars (Morris 1988, 1994; Morris et al. 2000). Isoclines are the curves in the species density phase space that separate regions with qualitatively different species distributions. For example, the 0% isocline for species A separates population densities of species A and B for which species A occupies only the second patch. Similarly, we can define the 100% isocline and other isoclines as well. The isodar for species A is the curve in the habitat 1–habitat 2 density phase space along which the expected fitness of individuals is identical in the two habitats (Morris 1988). Isodars can be extended for two species, in which case the plots are in the patch 1 versus patch 2 total species density phase space (Morris 1988, 1989). In other words, isodars are the equal fitness lines plotted in species density phase space. Relation between isolegs and isodars was studied by Morris (1999). However, neither Rosenzweig nor Morris went further to define and compute the IFD for two competing species for each fixed species densities. This was done by Křivan and Sirot (2002) using game theory. They defined two-species IFD over two habitats as the strategy that is the best response when played against itself (the first NE condition for ESS) and that is stable with respect to spatial perturbations, but the concept of stability was not clearly spelled out. The authors also assumed that interspecific competition is patch independent (i.e., the competition coefficients α and β are patch independent). Therefore, this article is the first study we are aware of that clearly defines the concept of IFD for two species. Moreover, this concept of IFD can be applied not only to competing species but also to predator-prey games where predators are searching for prey and prey try to avoid predators. The latter game was studied by Křivan (1997) and Křivan and Schmitz (2003) but only under the condition that there was no intraspecific competition between prey. Because their definition of a predator-prey IFD is actually a weak two-species ESS, the definition of IFD given in this article extends these previous works and allows intraspecific competition in the prey population, which is a nontrivial extension of those earlier works.

For further advancement of ecology, it is crucial to un-

derstand linkages between animal behavior and population dynamics. An important initial issue is whether the behavior of individuals influences the long-run outcome of the population dynamics. To this end, we compared two possibilities for individual behavior: either individuals move between habitats and rapidly settle at the IFD for current population size(s) or they are prevented from changing habitats (perhaps through a physical barrier separating the habitats, or perhaps individuals are completely immobile). For single-species models, we find no difference among the predictions either on the population or on the behavioral timescale. The equilibrial population abundance and the corresponding spatial distribution were the same regardless of whether animals could move between patches. That is, someone observing different two-habitat systems (each system corresponding to one of our two scenarios of individual behavior) with the same model parameters would see the same population distribution between the two habitats. It would require more careful observations to ascertain whether individual animals moved between habitats and, if so, at what rate these individuals changed the average amount of time they spent in each habitat. In particular, when we study population dynamical consequences of the IFD, we find that for a single population in an environment consisting of two or more resource patches, all patches will be occupied at the population equilibrium. This prediction differs from the IFD that does not consider population dynamics because the IFD predicts that at low population density, individuals will congregate in the best habitat, and additional habitats will be sequentially occupied as population size increases (Fretwell and Lucas 1970).

However, for two-species models, the eventual stable equilibrium population distribution does depend on whether individuals migrate. We have shown this clearly in the competitive species example for figure 6 that compares predictions with immobile animals to those with mobile animals. Here, two competing species that cannot move between habitats will eventually coexist in some equilibrial population densities in both habitats while mobile species segregate into separate habitats (fig. 6). This prediction shows that for two or more competing species, one cannot analyze the habitat selection in a species by analyzing the two separate habitats in isolation, as the single species model suggests. The reason for these discrepancies is the fact that for multiple species, the spatial species distribution may not be an IFD because it is not stable with respect to spatial perturbations at the corresponding stable species population equilibrium. Similarly, the population equilibrium that corresponds to an IFD may not be stable with respect to population dynamics (fig. 7). These discrepancies between long-term population stability versus short-term stability of species distribution

(i.e., population dynamics vs. game dynamics) are due to the fact that for population stability with immobile animals, we only need the strength of interspecific competition relative to that of intraspecific competition to be small in each habitat (this is the classical stability condition for the single habitat Lotka-Volterra competition model). However, for the stability of the species distribution when animals do migrate, not only these relative strengths but also the relative strengths between different habitats (e.g., products of the form $\alpha_1\beta_2$ in our notation) must be small enough because a single individual visits both patches during its lifetime.

On the other hand, we have shown that there are several special scenarios under which population and distribution stability lead to the same predictions. For example, if interspecific competition for both species is patch independent (which means that the coefficient for interspecific competition for species 1 is the same in both patches and similarly for species 2), then the population equilibrium for the model that does not assume migration between patches and the corresponding two-species distributions are also stable population equilibria and IFD when individuals do migrate between patches. Similarly, if interspecific competition is weak when compared with intraspecific competition across both patches, then the model with migration leads to the same stable population equilibrial densities and species distribution as the model without migration. Furthermore, for predator-prey interactions, population and distribution stability always lead to the same predictions.

To verify our theoretical predictions for two competing species, we can suggest the following experimental setup consisting of two different habitats occupied by two competing species. In one treatment, migration of the two species between habitats would be blocked, while in the other treatment, individuals could freely migrate. Provided differences in habitats are big enough so that inequality (10) holds and yet, for these same parameters, both species coexist in either habitat when migration is blocked, then we should observe changes in species distribution among habitats when individuals are allowed to migrate. Consequently, there will also be changes in population abundances. If inequality (10) does not hold, then both treatments should give the same results (i.e., equilibrium population abundances and population distribution should be the same whether individuals migrate). Similarly, for a single species or for predator-prey interactions, the two treatments should give the same results. Related experiments were done in the Western Negev Desert with two species of gerbils (Abramsky et al. 1991, 1994). In these experiments, isolegs and isoclines for *Gerbillus alenbyi* and *Gerbyllus pyramidum* were estimated. The experimental design consisted of two identical enclosures con-

nected by gates. Each of the two enclosures contained two habitat types: semistabilized and stabilized dunes. In one experiment (Abramsky et al. 1991), only *G. alenbyi* could migrate between the two enclosures, while in the other experiment (Abramsky et al. 1994), only *G. pyramidum* could pass through the gates. Manipulating species densities allowed for the experimental estimation of the IFD for the two species and also their population equilibrium (Abramsky et al. 1994). When at low abundance, both species showed clear preferences for the same habitat (semistabilized dune). As densities of the stronger competitor *G. pyramidum* increased, the weaker competitor (*G. alenbyi*) switched its preference for the alternative habitat (stabilized dune). At the population level, one stable population equilibrium and one unstable population equilibrium were predicted. The corresponding IFD at the stable population equilibrium predicted that the two species would segregate to different habitats. This clearly shows that there is an interplay between population dynamics and species distribution for which our theoretical results given in this article provide a testable hypothesis.

APPENDIX A

Competitive Species Population Dynamics

We linearize the population dynamics of equation (16) around an interior equilibrium (i.e., one where both species coexist in both habitats) for the two-species competition model. From equation (9), we compute for fixed population densities M and N

$$p_1 M = \frac{1}{C}[A(s_1 L_2 + s_2 L_1) - B(\alpha_1 r_1 K_2 + \alpha_2 r_2 K_1)],$$

$$q_1 N = \frac{1}{C}[B(r_1 K_2 + r_2 K_1) - A(\beta_1 s_1 L_2 + \beta_2 s_2 L_1)], \quad \text{(A1)}$$

where $A = (r_1 - r_2)K_1 K_2 + r_2 K_1(M + \alpha_2 N)$, $B = (s_1 - s_2)L_1 L_2 + s_2 L_1(\beta_2 M + N)$, and C is given by the left-hand side of inequality (10). Solving these expressions for p_1 and q_1 in terms of M and N and then substituting them into the right-hand side of equation (16) allows us to compute the corresponding population equilibrium (M^*, N^*) and check for its stability. The straightforward but tedious calculation produces the 2×2 Jacobian matrix $\mathbf{J}$ with entries

$$J_{11} = \frac{r_1 r_2 M^*[s_1 L_2(\alpha_1 \beta_1 - 1) + s_2 L_1(\alpha_2 \beta_2 - 1)]}{C},$$

$$J_{12} = \frac{r_1 r_2 M^*[\alpha_2 s_1 L_2(\alpha_1 \beta_1 - 1) + \alpha_1 s_2 L_1(\alpha_2 \beta_2 - 1)]}{C},$$

$$J_{21} = \frac{s_1 s_2 N^*[\beta_2 r_1 K_2(\alpha_1 \beta_1 - 1) + \beta_1 r_2 K_1(\alpha_2 \beta_2 - 1)]}{C},$$

$$J_{22} = \frac{s_1 s_2 N^*[r_1 K_2(\alpha_1 \beta_1 - 1) + r_2 K_1(\alpha_2 \beta_2 - 1)]}{C}.$$

$$\text{(A2)}$$

For asymptotic stability, we need $tr(\mathbf{J}) = J_{11} + J_{22} < 0$ and $\det(\mathbf{J}) = J_{11}J_{22} - J_{12}J_{21} > 0$.

These formulas simplify considerably when $\alpha_1 = \alpha_2 = \alpha$ and $\beta_1 = \beta_2 = \beta$. We get

$$C = (r_1 s_1 K_2 L_2 + r_1 s_2 K_2 L_1$$
$$+ r_2 s_1 K_1 L_2 + r_2 s_2 K_1 L_1)(1 - \alpha\beta),$$

$$tr(J) = [r_1 r_2 M^*(s_1 L_2 + s_2 L_1)$$
$$+ s_1 s_2 N^*(r_1 K_2 + r_2 K_1)]\frac{(\alpha\beta - 1)}{C},$$

$$\det(J) = -[r_1 r_2 M^*(s_1 L_2 + s_2 L_1)$$
$$\times s_1 s_2 N^*(r_1 K_2 + r_2 K_1)]\frac{(\alpha\beta - 1)^3}{C^2}.$$

The interior equilibrium is a two-species ESS (i.e., $C > 0$) if and only if the pure-strategy dynamic is asymptotically stable (i.e., $\alpha\beta < 1$) and if and only if the population dynamics with mobile consumers in equation (16) are asymptotically stable (i.e., $tr(J) < 0$ and $\det(J) > 0$).

APPENDIX B

Predator-Prey Population Dynamics

Following the same lines for competing populations, we find that an interior equilibrium for the predator-prey model is given by

$$p_1 = \frac{s_1 - s_2 + Ms_2\beta_2}{M(s_1\beta_1 + s_2\beta_2)},$$

$$q_1 = \frac{r_1 - r_2 + Nr_2\alpha_2}{N(r_1\alpha_1 + r_2\alpha_2)}$$

$$+ \sigma\frac{(s_2 - s_1)(K_1r_2 + K_2r_1) + M(s_1K_1r_2\beta_1 - s_2K_2r_1\beta_2)}{K_1K_2N(r_1\alpha_1 + r_2\alpha_2)(s_1\beta_1 + s_2\beta_2)}.$$

The Jacobian matrix **J** has the following entries:

$$J_{11} = -M^*\frac{r_1r_2(K_1s_1\alpha_1\beta_1 + K_2s_2\alpha_2\beta_2)\sigma}{K_1K_2(r_1\alpha_1 + r_2\alpha_2)(s_1\beta_1 + s_2\beta_2)},$$

$$J_{12} = -M^*\frac{r_1r_2\alpha_1\alpha_2}{r_1\alpha_1 + r_2\alpha_2},$$

$$J_{21} = N^*\frac{s_1s_2\beta_1\beta_2}{s_1\beta_1 + s_2\beta_2}, \qquad\qquad \text{(B1)}$$

$$J_{22} = 0.$$

Because $tr(\mathbf{J}) < 0$ and $\det(\mathbf{J}) > 0$ for $\sigma > 0$, it follows immediately that the interior equilibrium of the model with mobile predators and prey

$$M^* = \frac{1}{\beta_1} + \frac{1}{\beta_2},$$

$$N^* = \frac{1 - (\sigma/K_1\beta_1)}{\alpha_1} + \frac{1 - (\sigma/K_2\beta_2)}{\alpha_2}$$

is asymptotically stable when there is intraspecific competition among the prey.

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