



# The ideal free distribution as an evolutionarily stable state in density-dependent population games

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In classical games that have been applied to ecology, individual fitness is either density independent or population density is fixed. This article focuses on the habitat selection game where fitness depends on the population density that evolves over time. This model assumes that changes in animal distribution operate on a fast time scale when compared to demographic processes. Of particular interest is whether it is true, as one might expect, that resident phenotypes who use density-dependent optimal foraging strategies are evolutionarily stable with respect to invasions by mutant strategies. In fact, we show that evolutionary stability does not require that residents use the evolutionarily stable strategy (ESS) at every population density; rather it is the combined resident–mutant system that must be at an evolutionary stable state. That is, the separation of time scales assumption between behavioral and ecological processes does not imply that these processes are independent. When only consumer population dynamics in several habitats are considered (i.e. when resources do not undergo population dynamics), we show that the existence of optimal foragers forces the resident–mutant system to approach carrying capacity in each habitat even though the mutants do not die out. Thus, the ideal free distribution (IFD) for the single-species habitat selection game becomes an evolutionarily stable state that describes a mixture of resident and mutant phenotypes rather than a strategy adopted by all individuals in the system. Also discussed is how these results are affected when animal distribution and demographic processes act on the same time scale.

Classical models of game theory (e.g. the hawk–dove or prisoner's dilemma models) applied to biology assume that either population density (i.e. population size) is fixed or that individual fitness is density independent. In either case, individual fitness is then frequency dependent (i.e. the fitness of an individual using a given strategy depends only on the distribution of available strategies within the population). The biological game is then 'solved' by calculating the Nash equilibrium (NE; Nash 1951) or, if it exists, the evolutionarily stable strategy (ESS; Maynard Smith and Price 1973). The NE is the strategy which maximizes individual fitness in the sense that if all individuals in a given population use this strategy, then a mutant individual with another strategy cannot get a higher fitness. Thus, the NE captures Darwin's 'struggle for existence', because, through selection, an individual's fitness maximizes. The ESS, in addition to being a NE, requires that any other mutant strategy that does as well as the resident strategy cannot invade the resident population and must die out. If population size is not fixed and individual fitness is density independent, these models assume that once the game reaches its ESS solution, population density grows (or decays) exponentially at a rate given by the individual fitness. More realistic models of density-dependent population games (i.e. games that include both frequency and density effects on payoffs)

add a strategy-independent background fitness term that decreases with increasing density (Rowe et al. 1985, Cressman 1992). This term describes density dependence only (i.e. it is frequency independent), while the other term describes frequency dependence (i.e. this term is density independent). Argasinski and Kozłowski (2008) proposed that the two terms should be combined in a multiplicative way. However, in both the additive and the multiplicative cases, density dependence is selectively neutral because it affects all strategies in the same way. Thus, these cases do not model those population games where evolutionarily stable strategies change as population density changes, a situation that arises for the foraging games that we consider.

In this article, we assume that animal behavior operates on a short time scale when compared with a long time scale of population dynamics. Separating behavioral from population time scales allows us to assume that, at each fixed population size, the distribution of animal strategies is optimal (which is, in the game theoretical sense, an ESS). However, the complication here is that this strategy will change as the population densities change. This causes a complex feedback between animal behavior and population dynamics; animal behavior influences population dynamics which, in turn, changes animal behavior. In fact, the concept that combines animal behavior with population dynamics was already envisioned

by the famous ecologist, Evelyn Hutchinson (1965), who saw interacting individuals as actors in an evolutionary-ecological play in an ecological theater where each actor responds adaptively to changes in the strategy or abundance of the other actors. This led to the so called eco-evo perspective that recognizes the importance of the feed back between ecological and evolutionary processes for understanding of fundamental laws of biodiversity (reviewed by Day 2005). To build eco-evolutionary models one has to consider both population as well as evolutionary dynamics of changing traits.

To combine animal behavior with population dynamics and evolution we need to consider relevant time scales. Models that combine ecology and evolution often assume that evolutionary processes (i.e. changes in traits) run on a much slower time scale than population dynamics which allows for time scale separation. This area of research led to what is today known as 'adaptive dynamics' (reviewed by Vincent and Brown 2005, Dercole and Rinaldi 2008) (see also Waxman and Gavrillets 2005 and other articles in the same volume of the *Journal of Evolutionary Biology* devoted to adaptive dynamics). The trait dynamics are described by the so called 'canonical equation of adaptive dynamics' that models the evolution of monomorphic populations. Polymorphisms can also arise in adaptive dynamics through evolutionary branching (Dieckmann and Law 1996, Metz et al. 1996, Geritz et al. 1997, Kisdi 1999, Claessen and Dieckmann 2002).

A parallel line of research focused recently on the effect of plasticity in animal behaviors on population dynamics (reviewed by Miner et al. 2005). One example of such plastic behavior is optimal foraging theory (Stephens and Krebs 1986) that postulates the composition of animal diet when the proportion of prey in the environment changes. In contrast to adaptive dynamics, these studies assume that animal behavior runs on a faster time scale when compared to population time scale, i.e. at each population density, animal behavior is optimal in the sense that it maximizes individual fitness at a given population density. Thus, to unify plastic behaviors, population dynamics and evolutionary dynamics one needs to consider three time scales: individual, population, and evolutionary. In this article, we study the interactions between processes running on these three time scales by using the classical ecological concept of the ideal free distribution (IFD).

The IFD as defined by Fretwell and Lucas (1970) considered only the individual (short) time scale by assuming that animals disperse among patches in such a way that individual fitness in all occupied patches is the same. This concept ignored population dynamics by assuming a constant population size. It also ignored evolutionary time scale, because it did not consider stability of the resulting distribution with respect to invading mutants, i.e. to animals with different patch residence times. Recently, Cressman and Křivan (2006) (see also DeAngelis et al. 2007) proved that the IFD is indeed evolutionarily stable (i.e. an ESS) under the assumption that population numbers are fixed. In this article, we extend the concept of evolutionary stability for the IFD by assuming that the population undergoes dynamics. Thus, we consider all three time scales. The question that we ask here is whether mutants can or cannot invade if, at every population density, the corresponding resident strategy is an ESS that depends on these population numbers. In

particular, we will show that the expectation that all mutants necessarily die out in such systems is not true in general. Thus, to understand mechanisms that regulate biodiversity, it is necessary to combine animal behavior with population dynamics. That is, the simplified view by which time-scale separation allows us to study animal behavior and population dynamics independently does not yield a realistic model of evolutionary dynamics under invasion by mutants.

We document these general principles when behavioral dynamics are fast by analyzing a model of single-species foraging among several patches on resources that are at patch-dependent fixed levels. This approach corresponds, for example, to the classical logistic population growth model in each patch, where resource dynamics are not explicitly considered. If the fitness of an individual foraging in a given patch decreases as the density of foragers in this patch increases, it is well-known (Fretwell and Lucas 1970) that, for each fixed population density of foragers, there is a unique ideal free distribution (IFD). At this frequency distribution, individual fitness is the same in all occupied patches and no individual can increase fitness by moving to an unoccupied patch. Cressman and Křivan (2006) showed that the single species IFD is, for a fixed population density, an ESS in the original sense (Maynard Smith 1982) that a monomorphic resident population cannot be invaded by a small monomorphic mutant population. In this article, we first show that the IFD is also stable in polymorphic populations where there are several phenotypes. In this polymorphic setting we do not speak about evolutionarily stable strategies because no individual strategy corresponds to the (polymorphic) IFD, but the IFD is called an evolutionarily stable state (Hofbauer and Sigmund 1998). Then we analyze, as the population density changes, whether a monomorphic resident population that adopts the optimal IFD strategy is resistant to invasion by mutant individuals using a different strategy. Somewhat surprisingly, we will show that mutant strategies do not die out. In fact, they can survive in the system, although they cannot spread and outcompete the residents.

Mutant strategies can also survive in predator-prey models under fast behavioral dynamics when resident predators and/or prey show adaptive traits by being perfect optimizers. In fact, Křivan and Cressman (2009) show this phenomenon also occurs when the predator-prey population-trait dynamics converge on a limit cycle or a family of such cycles. However, they go on to show that the proportion of mutants is likely to decrease to zero when individual behavior of residents does not instantaneously track changing population densities and population dynamics do not settle on an equilibrium. In this paper, we examine whether these latter results hold in the multi-patch model where a single species evolves to its IFD at population equilibrium.

### Evolutionary stability of the IFD

Suppose we have a single species foraging among  $H$  patches. Let  $x$  be its population density and  $u = (u_1, \dots, u_H)$  ( $u_1 + \dots + u_H = 1$ ) be the distribution vector whose components give the proportion of this population in the different patches (i.e. there are  $u_i x$  resident foragers in patch  $i$ ). Due to competition, individual fitness in patch  $i$  is assumed to be a decreasing function ( $F_i$ ) of the number of foragers in this

patch. We also assume that each patch is characterized by its carrying capacity  $K_i$  (see Table 1 for the meaning of symbols used throughout this article). The spatial distribution  $u$  corresponds to the IFD provided fitness in all occupied patches is the same and at least as large as the fitness in unoccupied patches (Fretwell and Lucas 1970). Thus, the IFD distribution is defined by the condition  $F_j(u_j, x) \leq F_i(u_i, x)$  whenever  $1 \leq i, j \leq H$  and patch  $i$  is occupied (i.e.  $u_i \neq 0$ ). Indeed, let us consider two different occupied patches  $i$  and  $j$ . The above inequality must hold for both  $i$  and  $j$  (i.e. together with the above inequality we also get inequality where indexes  $i$  and  $j$  are reversed) which implies that  $F(u_i, x) = F(u_j, x) = \bar{F}$ . Moreover, if a patch  $j$  is not occupied, the above inequality implies that individuals who move to this patch from any occupied patch would necessarily lower their current fitness (even in the best case where an unoccupied patch has the same fitness as all occupied patches, by moving to this unoccupied patch, fitness there will decrease, making the patch worse than the other occupied patches). Since the IFD model assumes that there is no cost associated with moving from one patch to another, each resident individual is free to spend part of its time in different patches as long as the overall population distribution is  $u$ . Thus, the IFD is a property of a population and it does not tell us anything about individual strategies that lead to such a population distribution. Under the assumption that patch payoff decreases as population density in the patch increases, the IFD is unique for each population density  $x$  and it optimizes individual fitness given that the population distribution is  $u$ . Thus, a resident population where individuals behave adaptively must be distributed according to the IFD or else some individuals would have an incentive to change their strategy. It is worth noting that, as shown by Fig. 1 in Křivan et al. (2008), the IFD does not optimize population mean fitness given population density  $x$  (Morris 2003).

In this article, we consider two extreme individual strategies. The first follows the original idea of J. Maynard Smith and G. Price in that it assumes a monomorphic population where all individuals use the same strategy  $u = (u_1, \dots, u_H)$  giving the proportion of its lifetime that each individual spends in a given patch. In particular, this perspective assumes that individuals disperse frequently between patches which may be the case of many experimental setups where distance between patches is relatively small (Milinski 1979, Berec et al. 2006). The fitness of each individual is then  $W(u, u; x)$  where

$$W(v, u; x) = \sum_{i=1}^H v_i F_i(u_i, x) \quad (1)$$

is the fitness of a focal individual who uses strategy  $v$  in a population with density  $x$  whose average strategy is  $u$ . In Vincent and Brown (2005),  $W(v, u; x)$  is called the 'fitness generating function'. There, it is typically a non-linear function of the focal individual's strategy. Since the population is monomorphic with all individuals using strategy  $u$ ,  $W(u, u; x)$  is also the average mean fitness in the population. Thus, monomorphism is the simplest case that makes an explicit link between animal distribution and individual strategy.

On the other hand, there is empirical evidence that populations often consist of specialized individuals (Bolnick et al. 2003). In our context, this means that there is individual variance with respect to which patches to use. An extreme case is when individuals spend their entire life in a single patch. As there are  $H$  different patches, we have  $H$  different phenotypes depending on the patch the individual lives in. This means that the population is polymorphic in that individuals use different strategies. Since the strategy of an individual who spends all its life in a single patch is different from the IFD, we cannot identify individual strategies with animal distribution as in the monomorphic case. If  $x_i$  denotes the population abundance in patch  $i$ , the animal distribution is  $u = (u_1, \dots, u_H) = (x_1/x, \dots, x_H/x)$  and  $W(u, u; x)$  defined above becomes the average fitness in the population. In the polymorphic case, distribution  $u$  is interpreted as the 'resident population state' in accordance with the terminology used in evolutionary game theory (Hofbauer and Sigmund 1998). Under the IFD, all occupied patches are equally good and all resident individuals have the same fitness  $W$  which equals the average population fitness. The important observation is that regardless of whether the population is monomorphic or polymorphic as described above, under the IFD,  $W$  defined above is the individual fitness at population density  $x$ . In reality, we can also expect mixed cases where different behavioral morphs do not stay in a single patch but use more complex strategies. Regardless of this, the above analysis shows that  $W$  is the individual fitness under the IFD.

In the polymorphic case, where (most) individuals do not move between patches, a question naturally arises how the IFD can be achieved. In fact, whether the population is monomorphic or polymorphic, adaptive behavior will lead to the IFD (Cressman et al. 2004) at which the individual fitness  $W$  of everyone will be equal to population mean fitness  $\bar{F}$ . For instance, the standard model in the game theory literature, based on the replicator equation (Hofbauer and Sigmund 1998), demonstrates this result. This model assumes that the per capita population growth in each patch is equal to the fitness in the patch

$$\frac{dx_i}{dt} = x_i F_i(x_i) \quad (2)$$

where  $x_i = u_i x$  is population density in patch  $i$ . Then the replicator equation for the population distribution  $u$  is

$$\frac{du_i}{dt} = u_i (F_i(u_i, x) - \bar{F})$$

where  $\bar{F} = \sum_{i=1}^H u_i F_i(u_i, x)$  is the population mean fitness.

Here we use  $\bar{F}$  instead of  $W$  to distinguish between the population mean fitness and individual fitness (i.e. between polymorphism and monomorphism). It is clear that at the distributional equilibrium where the right hand side of the above equation is equal to zero, fitness in all occupied patches is the same and equal to the average fitness (i.e.  $F_i = \bar{F}$ ).

Table 1. List of symbols.

Symbol	Description
$F_i$	payoff in patch $i$
$\bar{F}$	average payoff across patches
$H$	number of patches
$K_i$	carrying capacity of patch $i$
$r_i$	per capita population growth rate in patch $i$
$u_i$	proportion of resident individuals in patch $i$
$\tilde{u}_i$	proportion of mutant individuals in patch $i$
$W(v, u; x)$	fitness of an individual using strategy $v = (v_1, \dots, v_H)$ in a resident population with (mean) strategy $u = (u_1, \dots, u_H)$ when overall number of individuals is $x$
$W(v, u; \tilde{u}, x, \tilde{x})$	fitness of an individual using strategy $v = (v_1, \dots, v_H)$ in a resident-mutant system with (mean) resident strategy $u = (u_1, \dots, u_H)$ when overall number of residents is $x$ and overall number of mutants with strategy $\tilde{u}$ is $\tilde{x}$
$x$	total number of resident individuals in all patches; $x = x_1 + \dots + x_H$ where $x_i$ is the number of residents in patch $i$
$\tilde{x}$	total number of mutants in all patches; $\tilde{x} = \tilde{x}_1 + \dots + \tilde{x}_H$ where $\tilde{x}_i$ is the number of mutant individuals in patch $i$

The replicator equation does not consider animal dispersal and, because it rests on the assumption that changes in population distribution  $u$  are solely due to changes in population numbers, both distribution and population dynamics run on the same time scale. In many cases, however, animals will disperse and dispersal over short distances often operates on a much shorter time scale than population dynamics. In what follows, although we do not specify the dispersal process explicitly, we will assume that the resultant behavioral dynamics are sufficiently fast with respect to population dynamics so that the resident animal distribution is always at the IFD. This means that the IFD instantaneously tracks the population size  $x$ , which makes it a function of  $x$  (see the next section where the IFD  $u(x)$  is given explicitly as a function of  $x$ ). We continue to assume that the per capita population growth rate is proportional to individual fitness. Because all occupied patches are equally good under the IFD, individual fitness is independent from the animal strategy and it is equal to the mean population fitness ( $\bar{F}$ ) which defines the overall population growth

$$\frac{dx}{dt} = x\bar{F} = x \sum_{i=1}^H u_i(x)F_i(u_i(x)x) \quad (3)$$

whether the population is monomorphic or polymorphic. Here  $u(x) = (u_1(x), \dots, u_H(x))$  denotes the IFD at population density  $x$ . We remark that for our model with fitness in each patch a decreasing function of patch density, the IFD is unique (Fretwell and Lucas 1970) and so for each population density  $x$  there is exactly one IFD  $u(x)$ . At the population equilibrium  $\bar{F} = F_i = 0$  in all occupied patches which implies that the resident system evolves to its carrying capacity  $K_i$  in each patch. Here the population distribution is  $u_i^* = K_i/K$  where  $K = K_1 + \dots + K_H$  is the total carrying capacity of the system.

Now the question is if, and in which sense, the population distribution  $u^*(K)$  that corresponds to the IFD at equilibrium

population density is stable with respect to invasions by mutants using a different strategy. We remark here that Cressman and Křivan (2006) proved that at fixed population density  $x$  the IFD  $u(x)$  is an ESS. According to the definition (Maynard Smith and Price 1973), this means that no monomorphic mutant population, that uses a different strategy, can invade a monomorphic resident population whose distribution (as well as strategy) corresponds to  $u(x)$ . Here we consider a different scenario in which the resident population distribution  $u$  depends on the mutant population size and strategy as well as on resident population density  $x$ . To examine this question, suppose that the resident system is invaded by (monomorphic) mutants that have density  $\tilde{x}$  and use a strategy  $\tilde{u}$  that may or may not depend on both densities  $x$  and  $\tilde{x}$ . We assume that these mutant behavioral morphs have the same fitness function  $F_i$  in patch  $i$  as residents (i.e. they are identical to residents except they use a different strategy). Thus, if the resident population distribution is  $u$ , every individual's fitness in patch  $i$  is  $F_i(u_i x + \tilde{u}_i \tilde{x})$ . Because we assume here that residents and mutants are ecologically equivalent (they differ only in their use of patches), they are also locally competitively neutral in the sense that their mutual competition coefficient in each patch where they compete for shared resources equals 1. However, as we will see in the next section (cf. model 8), different strategies of residents and mutants lead to different interspecific competition coefficients at the global spatial scale. If these residents behave adaptively, they will distribute themselves among the patches according to the IFD conditioned on the mutants being present. That is, the resident distribution  $u$  is the function of  $x$ ,  $\tilde{x}$  and  $\tilde{u}$  that satisfies  $F_i(u_i x + \tilde{u}_i \tilde{x}) \leq F_j(u_j x + \tilde{u}_j \tilde{x})$  whenever  $1 \leq i, j \leq H$  and  $u_i \neq 0$ . As before, all resident individuals will have the same fitness  $W = \sum_{i=1}^H u_i F_i(u_i x + \tilde{u}_i \tilde{x})$ . Furthermore, the mutant population is monomorphic with individual fitness  $\tilde{W} = \sum_{i=1}^H \tilde{u}_i F_i(u_i x + \tilde{u}_i \tilde{x})$ . Thus, the corresponding resident-mutant population dynamics become

$$\begin{aligned} \frac{dx}{dt} &= xW = x \sum_{i=1}^H u_i(x, \tilde{x}, \tilde{u}) F_i(u_i(x, \tilde{x}, \tilde{u})x + \tilde{u}_i \tilde{x}) \\ \frac{d\tilde{x}}{dt} &= \tilde{x}\tilde{W} = \tilde{x} \sum_{i=1}^H \tilde{u}_i F_i(u_i(x, \tilde{x}, \tilde{u})x + \tilde{u}_i \tilde{x}) \end{aligned} \quad (4)$$

It is proved in Appendix 1 that the proportion of mutants in the population cannot increase in time and the proportion of mutants with respect to residents ( $\tilde{x}/x$ ) tends to some constant  $k^*$  as  $t$  increases. Either  $k^* = 0$  which means that mutants die out, or  $k^* > 0$  in which case mutants survive in the population. In the following section of a logistically growing population, we show that the mutants always persist (i.e.  $k^* > 0$ ) in the resident-mutant system. Thus, the mutant strategy becomes absorbed as one of the individual strategies in an extended polymorphic resident system. Moreover, Appendix 1 also shows that the population densities in the resident-mutant system (Eq. 4) still evolve to carrying capacity in all patches.

In summary, the existence of adaptive residents who distribute themselves according to the IFD  $u$  (for given  $x$ ,  $\tilde{x}$  and  $\tilde{u}$ ) forces the population distribution to evolve to the

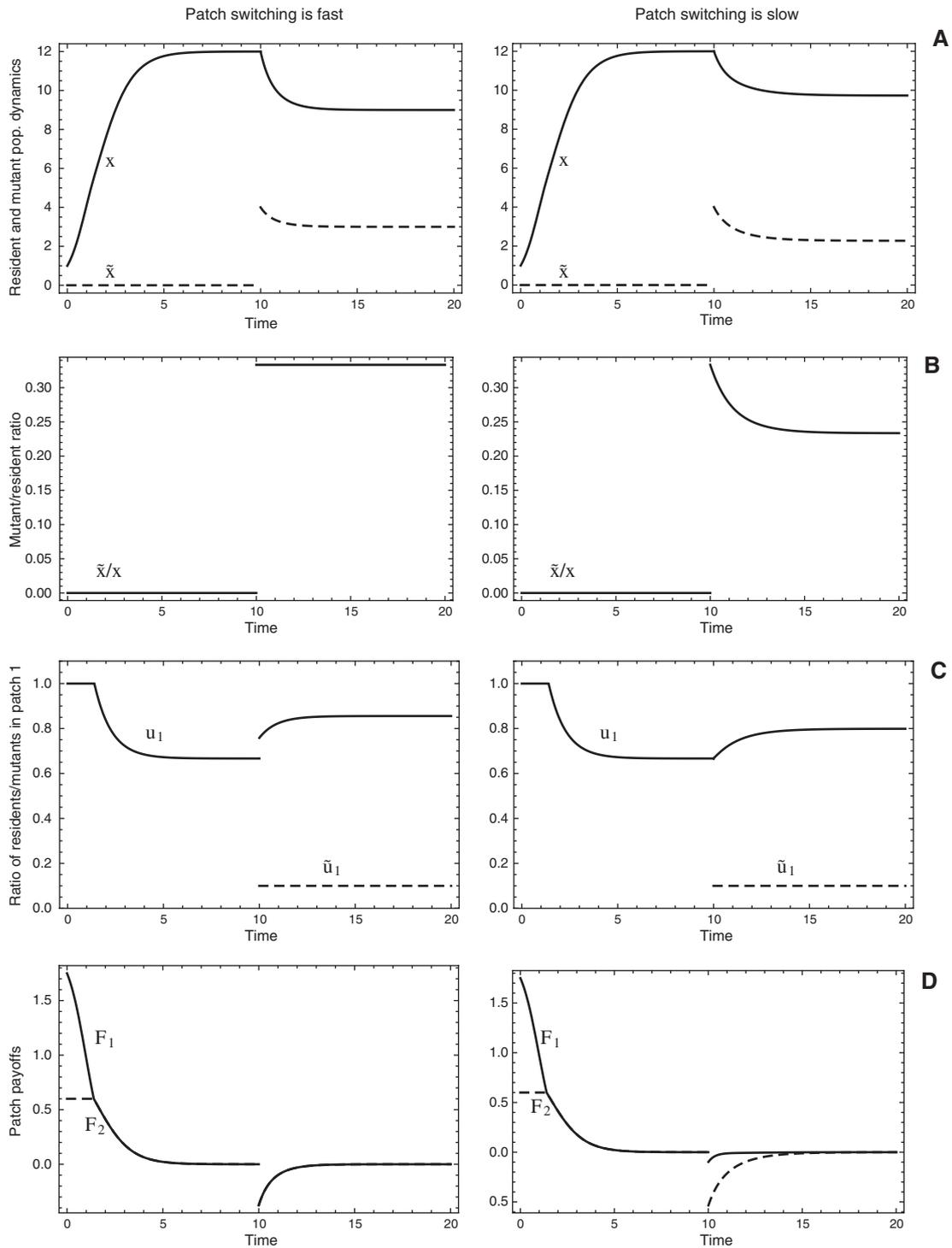


Figure 1. Simulation of the resident-mutant systems. The left panels assume that resident distribution tracks the IFD instantaneously (modeled by 10 and 11). The right panels assume that distribution tracks the IFD with some delay (modeled by 8 and 12). Panel A shows population dynamics of residents ( $x(t)$ , solid line) and mutants ( $\tilde{x}(t)$ , dashed line). Panel B shows the relative proportion  $\tilde{x}(t)/x(t)$  of mutants to residents. Panel C shows the strategy of residents ( $u_1(t)$ , solid line) and mutants ( $\tilde{u}_1(t)$ , dashed line), and panel D shows fitness  $F_i(t)$  in patch  $i$  ( $i = 1$ , solid line;  $i = 2$ , dashed line). Parameters used for simulations:  $r_1 = 2$ ,  $r_2 = 0.6$ ,  $K_1 = 8$ ,  $K_2 = 4$ ,  $\tilde{u}_1 = 0.1$ . There are only residents until time  $T = 10$ . Mutants enter at time  $T = 10$ , at which point residents are at the population equilibrium.

IFD  $u^*$  at the equilibrium population density  $K = K_1 + \dots + K_H$ . In this sense, the IFD is evolutionarily stable (i.e. an ESS). However, this form of evolutionary stability is different from the traditional meaning proposed by Maynard Smith (1982) whereby a monomorphic population using

the ESS forces any invading mutant subpopulation using another strategy to go extinct. As we have seen in our foraging model, even when the resident foragers are monomorphic, invading mutants need not die out but become part of an evolutionarily stable state. This phenomenon generalizes,

to density-dependent population games, the strong stability concept of frequency evolution (Cressman 1992, Hofbauer and Sigmund 1998) whereby the population state is evolutionarily stable at the ESS but individual mutant strategies persist and become part of the evolutionarily stable state. It also generalizes, to density-dependent population games, the result of Cressman and Křivan (2006) (see also Křivan et al. 2008) that the IFD is an ESS for single-species habitat selection games that assume fixed population density. That is, the IFD is evolutionarily stable as a population state rather than as an individual strategy.

These results suggest that, in studies of animal distribution that correspond to the IFD, it is not necessary to know what are the individual strategies, i.e. if the population is mono- or polymorphic. However, when movement between patches is limited (e.g. distance between patches is large) and animals seldom if ever disperse, then we are closer to the polymorphic case and cannot exclude the appearance of other, not yet observed behavioral morphs, in the future. Since strategies are identified with patches, a mutant strategy can only appear in patches that are unoccupied by residents. Moreover, mutants that survive eventually have the same fitness as residents, opening the door to future speciation through allopatry. On the other hand, the continued survival of mutants in a monomorphic resident system indicates different morphs can coexist simultaneously in the same patch, a situation conducive to sympatric speciation.

## Two patch logistic growth model

As an example, we consider two patches with a logistically growing population. In this case, the fitness in patch  $i$  ( $i = 1, 2$ ) is  $F_i(u, x) = r_i(1 - u_i x / K_i)$ , where  $u = (u_1, u_2)$ ,  $u_1 + u_2 = 1$ . We assume that the intrinsic per capita population growth rate in patch 1 is higher than in patch 2 ( $r_1 > r_2$ ).

From (Eq. 1), the fitness of a mutant with strategy  $v$  in the resident population (with strategy  $u$  and density  $x$ ) is the average of individual payoffs in each patch weighted by the proportion of time spent in each patch. That is

$$W(v, u; x) = v_1 r_1 \left(1 - \frac{u_1 x}{K_1}\right) + v_2 r_2 \left(1 - \frac{u_2 x}{K_2}\right)$$

which is linear in  $v$  and in  $u$ . Thus, the fitness is given as the average weighted sum of the per capita population growth rates during an individual lifetime. The resident population dynamics (Eq. 3) for the overall population density  $x = x_1 + x_2$  can be represented in the following matrix form

$$\frac{dx}{dt} = x \langle u(x), A(x)u(x) \rangle \quad (5)$$

where  $\langle v, u \rangle = v_1 u_1 + v_2 u_2$  stands for the scalar product of vectors  $v = (v_1, v_2)$  and  $u = (u_1, u_2)$ , and

$$A(x) = \begin{pmatrix} r_1 \left(1 - \frac{x}{K_1}\right) & r_1 \\ r_2 \left(1 - \frac{x}{K_2}\right) & r_2 \end{pmatrix}$$

To obtain matrix  $A$ , we write  $W(v, u; x)$  as a sum of terms in  $v_i u_j$  by substituting  $u_1 + u_2$  for 1 as follows

$$\begin{aligned} W(v, u; x) &= v_1 r_1 \left(u_1 + u_2 - \frac{u_1 x}{K_1}\right) + v_2 r_2 \left(u_1 + u_2 - \frac{u_2 x}{K_2}\right) \\ &= r_1 \left(1 - \frac{x}{K_1}\right) v_1 u_1 + r_1 v_1 u_2 + r_2 v_2 u_1 \\ &\quad + r_2 \left(1 - \frac{x}{K_2}\right) v_2 u_2 \end{aligned}$$

The entries of payoff matrix  $A$  are then the coefficient of the corresponding term in this expansion (i.e.  $A_{ij}$  is the coefficient of  $v_i u_j$ ). This method extends to produce payoff matrices for any number of patches whenever  $W(v, u; x)$  is linear in  $v$  and  $u$ . Although matrix games often describe situations with pair-wise interactions (e.g. the hawk-dove game), our game does not fall in this category, because here a single individual plays against the population distribution. However, individual fitness is linear in mutant and resident strategy which allows to write it in a matrix form.

Writing population dynamics in the form given by (Eq. 5) is convenient because it allows immediate calculation of the ESS/IFD strategy (thus  $u(x)$ ) for any population density  $x$ . It follows from game theory for matrix games (Weibull 1995, Hofbauer and Sigmund 1998) that the strategy to occupy patch one only (i.e.  $u_1 = 1$ ) is the ESS provided  $A_{11}(x) > A_{21}(x)$  which happens when population density is low ( $x \leq K_1(r_1 - r_2)/r_1$ ). For higher densities, both patches will be occupied, fitness will be the same ( $F_1(u_1 x) = F_2(u_2 x)$ ), and

$$u_1(x) = \frac{r_2 K_1}{r_2 K_1 + r_1 K_2} + \frac{K_1 K_2 (r_1 - r_2)}{(r_2 K_1 + r_1 K_2) x} \quad (6)$$

(Křivan and Sirot 2002). Substitution of this ESS strategy into the resident system (Eq. 5) yields (Appendix 2)

$$\frac{dx}{dt} = \begin{cases} r_1 x \left(1 - \frac{x}{K_1}\right) & \text{if } x < \frac{K_1(r_1 - r_2)}{r_1} \\ \frac{r_1 r_2 x}{K_2 r_1 + K_1 r_2} (K_1 + K_2 - x) & \text{if } x \geq \frac{K_1(r_1 - r_2)}{r_1} \end{cases} \quad (7)$$

Thus, the overall population abundance  $x$  converges to  $K_1 + K_2$  and the corresponding population distribution is  $u_1 = K_1 / (K_1 + K_2)$ .

Following our general treatment of evolutionary stability of the IFD in several patches, we are now interested in the following question: Is it possible that a resident population that plays the ESS can be invaded by a mutant population with a different strategy? Indeed, this question is non-trivial because the resident strategy leads to a population distribution under which all patches provide the same payoff. Thus, a mutant with a different strategy will receive the same payoff as residents. It seems there is no mechanism that could prevent mutants from invading the resident system. What remains unclear is whether mutants can replace residents as well. We now show this cannot happen by describing the dynamics of the resident-mutant system (Eq. 4) for the case of the logistic population growth in two patches.

Consider a small mutant population with population density  $\tilde{x}$  and a fixed strategy  $\tilde{u} = (\tilde{u}_1, \tilde{u}_2)$  in a resident system with density  $x$  and strategy  $u$ . The fitness of an individual using strategy  $v = (v_1, v_2)$  is then

$$W(v, u; \tilde{u}, x, \tilde{x}) = v_1 r_1 \left( 1 - \frac{u_1 x + \tilde{x} \tilde{u}_1}{K_1} \right) + v_2 r_2 \left( 1 - \frac{u_2 x + \tilde{x} \tilde{u}_2}{K_2} \right)$$

which is also linear in  $v$  and in  $u$ . This form is again convenient to get resident-mutant population dynamics (Eq. 4) since  $W(u, u; \tilde{u}, x, \tilde{x})$  defines the per capita resident population growth rate while  $W(\tilde{u}, u; \tilde{u}, x, \tilde{x})$  defines the per capita mutant population growth rate. The resident-population dynamics (Eq. 4) are then (Appendix 2)

$$\begin{aligned} \frac{dx}{dt} &= x W(u, u; \tilde{u}, x, \tilde{x}) = x \left\langle u, A(x, \tilde{x}, \tilde{u}) u \right\rangle \\ &= (r_1 u_1 + r_2 u_2) x \left( 1 - \frac{x}{k_1} - \frac{\alpha}{k_1} \tilde{x} \right) \\ \frac{d\tilde{x}}{dt} &= \tilde{x} W(\tilde{u}, u; \tilde{u}, x, \tilde{x}) = \tilde{x} \left\langle \tilde{u}, A(x, \tilde{x}, \tilde{u}) u \right\rangle \\ &= (r_1 \tilde{u}_1 + r_2 \tilde{u}_2) \tilde{x} \left( 1 - \frac{\tilde{x}}{k_2} - \frac{\beta}{k_2} x \right) \end{aligned} \quad (8)$$

where

$$A(x, \tilde{x}, \tilde{u}) = \begin{pmatrix} r_1 \left( 1 - \frac{x + \tilde{u}_1 \tilde{x}}{K_1} \right) & r_1 \left( 1 - \frac{\tilde{u}_1 \tilde{x}}{K_1} \right) \\ r_2 \left( 1 - \frac{\tilde{u}_2 \tilde{x}}{K_2} \right) & r_2 \left( 1 - \frac{x + \tilde{u}_2 \tilde{x}}{K_2} \right) \end{pmatrix}$$

Here

$$\begin{aligned} k_1 &= \frac{K_1 K_2 (r_1 u_1 + r_2 u_2)}{K_2 r_1 u_1^2 + K_1 r_2 u_2^2} \text{ and } k_2 = \frac{K_1 K_2 (r_1 \tilde{u}_1 + r_2 \tilde{u}_2)}{K_2 r_1 \tilde{u}_1^2 + K_1 r_2 \tilde{u}_2^2} \\ \alpha &= \frac{K_2 r_1 u_1 \tilde{u}_1 + K_1 r_2 u_2 \tilde{u}_2}{K_2 r_1 u_1^2 + K_1 r_2 u_2^2} \text{ and } \beta = \frac{K_2 r_1 u_1 \tilde{u}_1 + K_1 r_2 u_2 \tilde{u}_2}{K_2 r_1 \tilde{u}_1^2 + K_1 r_2 \tilde{u}_2^2} \end{aligned}$$

can be interpreted as the global environmental carrying capacity for residents ( $k_1$ ) and mutants ( $k_2$ ) as well as the global interspecific competition coefficients ( $\alpha$  and  $\beta$ ). These parameters depend on the strategy of residents and mutants. From this perspective, (Eq. 8) generalizes the classical Lotka-Volterra competition equations to the resident-mutant system in a two-patch environment.

First, consider for a moment the case where residents are not adaptive. That is, both residents and mutants use fixed strategies  $u$  and  $\tilde{u}$  for all population sizes. Then the resident-mutant dynamics (Eq. 8) is the classical two-species competitive system where either both species coexist at the equilibrium, or one species outcompetes the other species. If residents and

mutants show distinct preferences for the two patches with respect to patch carrying capacities, (i.e. if  $(\tilde{u}_1 - K_1/(K_1 + K_2))(\tilde{u}_1 - K_1/(K_1 + K_2)) < 0$ ), then the resident-mutant dynamics has a positive coexistence equilibrium  $(\tilde{x}, \tilde{x}^*)$  at

$$\begin{aligned} E &= \left( \frac{k_1 - k_2 \alpha}{1 - \alpha \beta}, \frac{k_2 - k_1 \beta}{1 - \alpha \beta} \right) \\ &= \left( \frac{K_1 - (K_1 + K_2) \tilde{u}_1}{u_1 - \tilde{u}_1}, \frac{(K_1 + K_2) u_1 - K_1}{u_1 - \tilde{u}_1} \right) \end{aligned}$$

Moreover, since  $0 < \alpha \beta < 1$  when  $u_1 \neq \tilde{u}_1$ , this equilibrium is globally asymptotically stable (in particular, all initial positive distributions converge to it). That is, the fitness of all individuals at the equilibrium is the same and equals 0. By linearity of the fitness functions, to satisfy the two equations for population equilibrium (i.e.  $W(u, u; \tilde{u}, x, \tilde{x}) = W(\tilde{u}, u; \tilde{u}, x, \tilde{x}) = 0$ ), payoffs in both patches must be the same and equal to zero (i.e.  $r_1(1 - (u_1 x^* + \tilde{u}_1 \tilde{x}^*)/K_1) = r_2(1 - (u_2 x^* + \tilde{u}_2 \tilde{x}^*)/K_2) = 0$ ) at the population equilibrium. Thus, the animal distribution converges to the IFD. This analysis shows that the IFD will be reached at the population equilibrium even if animals do not show any adaptive behaviors. However, the IFD will be reached only at the population equilibrium and not along the population trajectory. When  $(u_1 - K_1/(K_1 + K_2))(\tilde{u}_1 - K_1/(K_1 + K_2)) > 0$ , there is no positive equilibrium and either  $x$  or  $\tilde{x}$  converge to 0. Appendix 2 shows that the population with strategy that better matches the IFD will survive. Thus, if mutant strategy is closer to the IFD when compared to the resident strategy, mutants will invade, otherwise they will die out.

Second, we consider the case where residents instantaneously track the IFD. The optimal resident strategy becomes a function of both mutant density and strategy. Let us assume that when residents are at low densities the first patch is more profitable for them. This will be when mutant density is small. As resident numbers in patch 1 increase, there will be a critical density  $x^1$  at which both patches will provide the same payoff, i.e.  $A_{11}(x, \tilde{x}, \tilde{u}) = A_{21}(x, \tilde{x}, \tilde{u})$ . Then for small population densities that satisfy  $x < x^1$ ,  $A_{11} > A_{21}$  and the resident optimal strategy is to be in patch 1 only. In other words, for low consumer densities the entries in the first row of the matrix  $A$  are larger than the corresponding entries in the second row so that the strategy to stay in patch 1 is dominant over all possible strategies. In the case  $x^1$  is negative, the solution of  $A_{12}(x, \tilde{x}, \tilde{u}) = A_{22}(x, \tilde{x}, \tilde{u})$  that we denote as  $x^2$  is positive. (We remark, that subtracting the two equalities  $A_{11}(x^1, \tilde{x}, \tilde{u}) = A_{21}(x^1, \tilde{x}, \tilde{u})$  and  $A_{12}(x^2, \tilde{x}, \tilde{u}) = A_{22}(x^2, \tilde{x}, \tilde{u})$  yield  $r_1 K_2 x^1 + r_2 K_1 x^2 = 0$ . Thus, it is impossible that  $x^1$  and  $x^2$  are both positive). This can happen only when mutants show strong preferences for patch 1. Once again, if  $x < x^2$ ,  $A_{22} > A_{12}$  and the optimal strategy is to be in patch 2 only. By direct calculation, we find

$$\begin{aligned} x^1 &= \frac{K_1(r_1 - r_2)}{r_1} + \frac{(r_2 K_1 - \tilde{u}_1(K_2 r_1 + K_1 r_2)) \tilde{x}}{r_1 K_2} \\ \text{and} \\ x^2 &= -\frac{K_2(r_1 - r_2)}{r_2} - \frac{(r_2 K_1 - \tilde{u}_1(K_2 r_1 + K_1 r_2)) \tilde{x}}{r_2 K_1} \end{aligned}$$

For  $x \geq \max\{x^1, x^2\}$ , the optimal resident strategy satisfies  $F_1(u_1 x + \tilde{u}_1 \tilde{x}) = F_2(u_2 x + \tilde{u}_2 \tilde{x})$  which gives

$$u_1 = \frac{r_2 K_1}{r_2 K_1 + r_1 K_2} + \frac{K_1 K_2 (r_1 - r_2)}{(r_2 K_1 + r_1 K_2) x} + \frac{(K_1 r_2 - \tilde{u}_1 (K_1 r_2 + K_2 r_1)) \tilde{x}}{(K_1 r_2 + K_2 r_1) x} \quad (9)$$

That is, model 8 becomes

$$\frac{dx}{dt} = \begin{cases} r_1 x \left(1 - \frac{x + \tilde{u}_1 \tilde{x}}{K_1}\right) & \text{if } 0 < x < x^1 \\ r_2 x \left(1 - \frac{x + \tilde{u}_2 \tilde{x}}{K_2}\right) & \text{if } 0 < x < x^2 \\ \frac{r_1 r_2 x}{K_2 r_1 + K_1 r_2} (K_1 + K_2 - x - \tilde{x}) & \text{if } x \geq \max\{x^1, x^2\} \end{cases} \quad (10)$$

and

$$\frac{d\tilde{x}}{dt} = \begin{cases} r_1 \tilde{u}_1 \tilde{x} \left(1 - \frac{x + \tilde{u}_1 \tilde{x}}{K_1}\right) + r_2 \tilde{u}_2 \tilde{x} \left(1 - \frac{\tilde{u}_2 \tilde{x}}{K_2}\right) & \text{if } 0 < x < x^1 \\ r_1 \tilde{u}_1 \tilde{x} \left(1 - \frac{\tilde{u}_1 \tilde{x}}{K_1}\right) + r_2 \tilde{u}_2 \tilde{x} \left(1 - \frac{x + \tilde{u}_2 \tilde{x}}{K_2}\right) & \text{if } 0 < x < x^2 \\ \frac{r_1 r_2 \tilde{x}}{K_2 r_1 + K_1 r_2} (K_1 + K_2 - x - \tilde{x}) & \text{if } x \geq \max\{x^1, x^2\} \end{cases} \quad (11)$$

The coupled dynamics 10 and 11 are illustrated in Fig. 1, left panels, when the initial resident density  $x(0)$  is small ( $0 < x(0) < x^1$ ) and there are no mutants. For an initial time interval (approximately  $0 \leq t \leq 2$ ), the fitness in patch 1 is larger than in patch 2 ( $r_1 (1 - \frac{x}{K_1}) > r_2$ , panel D); and all residents occupy patch 1 only ( $u_1^1 = 1$ , panel C). As the resident population increases, some resident individuals will eventually (for  $t \geq 2$ ) occupy the other patch (panel C) and, due to their adaptive behavior, both patches will provide the same fitness (panel D). Total population size converges to  $K_1 + K_2$  ( $= 12$  in panel A) and population mean fitness approaches 0 (panel D). At time  $t = 10$ , mutants with fixed preferences for either patch ( $\tilde{u}_1 = 0.1$ ,  $\tilde{u}_2 = 0.9$ ) enter the resident system. These mutants survive in the system (panel A, Appendix 3) and residents adjust their distribution (panel C) so that both patches remain equally good (panel D). Moreover, the proportion of mutants to residents does not change (panel B).

The reason why mutants survive in the system together with residents is that the instantaneous redistribution of residents keeps fitness in both patches the same (Fig. 1, left panel D). As both patches are equally profitable, fitness of any mutant is independent of its strategy and it is equal to resident fitness. Thus, there is no selection pressure against mutants. This shows that time scale separation can be important in predicting the effects of adaptive behaviors. For example, if both behavior and population dynamics run

on the same time scale there will be more time to exclude mutants from the system because fitness in the two patches will not be the same for a while.

Indeed, the right panels of Fig. 1 show the situation where patch switching is modeled explicitly by

$$\frac{du_1}{dt} = u_1^* - u_1 \quad (12)$$

where  $u_1^*$  is the optimal strategy given through (9) as

$$u_1^* = \min \left\{ \begin{aligned} &1, \frac{r_2 K_1}{K_2 r_1 + K_1 r_2} + \frac{K_1 K_2 (r_1 - r_2)}{x (r_2 K_1 + K_2 r_1) x} \\ &+ \frac{(K_1 r_2 - \tilde{u}_1 (K_1 r_2 + K_2 r_1)) \tilde{x}}{(K_1 r_2 + K_2 r_1) x} \end{aligned} \right\}$$

That is,  $u_1$  is moving in the direction of the optimal strategy at each population size on the same time scale as the population dynamics. Thus, the animal distribution lags behind their optimal strategy and the two patches provide animals with a different fitness. Therefore, there is a selection gradient against mutants with a lower fitness and the proportion of mutants decreases (Fig. 1, right panel B). However, as population dynamics converge to an equilibrium, this selection gradient disappears (because, at the equilibrium, payoff in both patches are zero) and the numerical simulations show that, despite slow behavioral dynamics, mutants do survive in the system (Fig. 1, right panels A and B).

The analysis in this section for two-patch logistic growth can be extended to non-logistic and/or multi-patch models that include population dynamics. In fact, for these foraging models at fixed resource levels, it can be shown by extending the above arguments that mutants survive in the system. This is because, once the fitness in patches occupied by mutants equalizes due either to the dispersal of adaptive residents or to the convergence of the population dynamics to equilibrium, mutants and residents have the same fitness. Since there is then no selective force that would drive mutants to extinction, mutants will survive.

## Discussion

This article combines models of three major avenues of ecological research: behavioral models with population and evolutionary models. Our models are based on behavioral effects that attenuate very rapidly (in fact instantaneously) when compared to longer-term population dynamics. This view is reflected in our modeling approach by the assumption that animal behavior quickly reaches its stable equilibrium (that is often an evolutionarily stable strategy) at every population density. From the evolutionary point of view this means that no mutants using another strategy can invade at this ESS. If the above time scale argument prevents any interactions between behavior and population dynamics, then adding slow population dynamics should not qualitatively change this prediction. However, in this article, we show this is not so because even slow population changes

can allow new mutant strategies to evolve and survive in the population. This shows that the static concept of evolutionary stability, that is so often used in ecology, may not fully capture the stability concept when population dynamics are considered. That is, to understand mechanisms that regulate population stability, behavioral models must be combined with population dynamical models. The models analyzed in this article serve to dispel the notion that behavioral effects attenuate on much longer population or evolutionary time-scales. We call such models population games because they combine static equilibrium concepts from game theory with population dynamics.

In this article, we extend the game-theoretical evolutionary stability concept to models of population ecology where the static definition of an ESS (Maynard Smith and Price 1973) does not immediately apply. First, we show that once this ESS depends on population density through population dynamics, mutants can survive in the resident population. For the habitat selection game (Křivan et al. 2008), we show that, although the IFD is an evolutionarily stable strategy (Cressman and Křivan 2006) for every fixed population size, new mutants are not eliminated from the system when population dynamics are considered. The IFD is evolutionarily stable in the sense that the population distribution converges to it provided animals are adaptive. However, this form of evolutionary stability is different from the traditional meaning proposed by Maynard Smith (1982) whereby a monomorphic population using the ESS forces any invading mutant subpopulation using another strategy to go extinct. As we see in our optimal foraging model, even when the resident foragers are monomorphic, invading mutants do not die out but become part of an evolutionarily stable state. In particular, the combined resident-mutant system evolves to the unique IFD at the equilibrium population density whereby each habitat is occupied at its carrying capacity. On the other hand, the existence of adaptive residents prevents the number of mutants from increasing relative to the number of residents, i.e. although mutants do not go extinct they cannot completely replace residents either.

Our modeling approach to optimal adaptive foraging assumes that individual residents change their behavior on a much faster time scale than the population dynamics change species densities. That is, our evolutionary players act rapidly in Hutchinson's (1965) ecological theater. This is reasonable for our models where individual behavior is characterized by choice of habitat. Several experimental setups where distance between patches is relatively small (Milinski 1979, Parker and Sutherland 1986, Berec et al. 2006) conform to this assumption. Evolution of phenotypes that are behaviorally flexible (i.e. evolution of phenotypic plasticity; Schlichting and Pigliucci 1998, Miner et al. 2005) requires changes in genotypes and runs on an evolutionarily (slow) time scale. For such systems, the adaptive dynamics method (Dieckmann and Law 1996, Geritz et al. 1998, Abrams 2001, Cressman and Hofbauer 2005, Vincent and Brown 2005, Dercole and Rinaldi 2008) seems more suitable. Here, population densities quickly attain equilibrium values for current phenotypes and the main point of interest is the dynamics of population behavior that is described by the canonical equation of adaptive dynamics.

Interestingly, for both time scale extremes (i.e. for optimal foraging models where there is rapid behavioral change and for models of adaptive dynamics where phenotypic evolution is based on slow genetic change), the evolutionary stability of individual behavior is emphasized in order to predict the eventual outcome of the biological system. Moreover, we have argued that optimal foraging behavior promotes speciation and it is well-known (Dieckmann et al. 2004, Dercole and Rinaldi 2008) that speciation occurs in adaptive dynamics models when monomorphic populations converge to an equilibrium that is not evolutionarily stable. Such parallels between these two extremes suggest a game-theoretic approach that combines three time scales (behavioral, population and evolutionary) deserves future research as the proper venue for Hutchinson's ecological theater.

We have also briefly considered the two-patch logistic model when the resident behavioral and the population dynamics operate on the same time scale. Although the proportion of mutant strategists may strictly decrease initially, they do not die out completely since individual fitness is necessarily zero in both patches as the resident-mutant system converges to the population equilibrium. Slight perturbations will keep the population size slightly out of the equilibrium, but patch payoffs will be only slightly different from zero. Therefore the selection gradient (see the right hand side of expression 13 for  $\tilde{x}/x$  in Appendix 1) will be small and, as our simulations given in the right panels of Fig. 1 show, mutants will survive in the system. This result differs from the analysis of evolutionary stability in predator-prey systems (where each species has at most two possible traits) by Křivan and Cressman (2009) when fast behavioral dynamics lead to cyclic population-trait dynamics. In these circumstances, they show that the proportion of mutants is likely to decrease to zero if residents do not instantaneously track their optimal strategy. This is because animal fitness along a population cycle is no longer zero as it is necessarily at a population equilibrium. If some perturbations drive population dynamics slightly off the predator-prey limit cycle, patch payoffs will not be the same and adaptive individuals will get a higher fitness when compared with non-adaptive mutants. Thus, there will be a positive selection against mutants for these predator-prey models.

Our result that the proportion of mutants cannot spread in a resident-mutant system when residents exhibit phenotypic plasticity by tracking an optimal strategy (Appendix 1) is a general principle for density-dependent population games (Křivan and Cressman 2009). From this perspective, evolutionary stability in models of habitat choice serve as a particular example of a wider phenomenon. However, these models have the additional property that there is a single optimal strategy at each population density; namely, the IFD. This is not always the case, even when individuals are restricted to two possible strategies. For example, in the multipopulation habitat selection game where two species are competing in a two patch environment (Křivan and Sirot 2002, Cressman et al. 2004, Křivan et al. 2008). In these games multiple IFDs can coexist which then leads to complex distributional-population dynamics (Abrams et al. 2007). It is likely that in these games the resident-mutant systems will not evolve to a population equilibrium which, in turn, can lead to selection against mutants.

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## Appendix 1

In the article we claim that mutant foragers cannot spread in the population when residents instantaneously track their optimal strategy and that overall population density approaches carrying capacity in each patch. To prove these facts, let  $\bar{F} = F_i(u_i x + \tilde{u}_i \tilde{x})$  for some  $u_i \neq 0$ . Then  $F_j(u_j x + \tilde{u}_j \tilde{x}) \leq \bar{F}$  if  $u_j = 0$  since  $u = (u_1, \dots, u_H)$  ( $u_i \geq 0$ ,  $u_1 + \dots + u_H = 1$ ) is the IFD. Thus, from model 3 and 4 combined with the quotient rule

$$\begin{aligned} \frac{d(\tilde{x}/x)}{dt} &= \frac{1}{x^2} \left( \frac{d\tilde{x}}{dt} x - \frac{dx}{dt} \tilde{x} \right) \\ &= \frac{1}{x^2} \left( x\tilde{x} \sum_{i=1}^H \tilde{u}_i F_i(u_i x + \tilde{u}_i \tilde{x}) - \tilde{x}x \sum_{i=1}^H \tilde{u}_i F_i(u_i x + \tilde{u}_i \tilde{x}) \right) \\ &= \frac{\tilde{x}}{x} \sum_{i=1}^H (\tilde{u}_i - u_i) F_i(u_i x + \tilde{u}_i \tilde{x}) \\ &= \frac{\tilde{x}}{x} \left( \sum_{i=1, u_i \neq 0}^H (\tilde{u}_i - u_i) F_i(u_i x + \tilde{u}_i \tilde{x}) + \sum_{j=1, u_j=0}^H \tilde{u}_j F_j(u_j x + \tilde{u}_j \tilde{x}) \right) \\ &\leq \frac{\tilde{x}}{x} \left( \sum_{i=1, u_i \neq 0}^H (\tilde{u}_i - u_i) \bar{F} + \sum_{i=1, u_i=0}^H \tilde{u}_i \bar{F} \right) = 0 \end{aligned} \quad (13)$$

Since  $V(x, \tilde{x}) = \tilde{x}/x$  is positive for  $\tilde{x} > 0$  and has a unique minimum at  $\tilde{x} = 0$ ,  $V$  is a (non-strict) Lyapunov function (Hofbauer and Sigmund 1998) for the resident-mutant system (Eq. 4) (i.e.  $dV/dt \leq 0$ ). Thus, along each trajectory  $(x(t), \tilde{x}(t))$  of Eq. 4,  $\tilde{x}/x$  has a limit  $k^* \geq 0$  and, at any  $\omega$ -limit point (that is, at any point that is a limit of points on the trajectory for a sequence of times approaching infinity)  $\frac{d(\tilde{x}/x)}{dt} = 0$ .

Furthermore,  $F_j(u_j x + \tilde{u}_j \tilde{x}) = \bar{F}$  for all  $j$  with  $u_j x + \tilde{u}_j \tilde{x} > 0$  at each  $\omega$ -limit point  $(x_0, k^* x_0)$ . This follows from the fact that if  $F_j(u_j x + \tilde{u}_j \tilde{x}) < \bar{F}$  for some  $j$  at an  $\omega$ -limit point then  $\frac{d(\tilde{x}/x)}{dt} < 0$  at this point which is not possible. Thus,

by Eq. 4,  $\frac{d(x + \tilde{x})}{dt} = (x + \tilde{x})\bar{F}$  for the trajectory starting at

$(x_0, k^* x_0)$ . Now, along this trajectory,  $\bar{F} > 0$  (respectively,  $\bar{F} < 0$ ) if  $x + \tilde{x}$  is less than (respectively, greater than) the carrying capacity  $K = K_1 + \dots + K_H$  and so  $x + \tilde{x}$  evolves monotonically to  $K$ . Therefore,  $x + \tilde{x} = K$  and  $\bar{F} = 0$  at one  $\omega$ -limit point  $(x^*, \tilde{x}^*)$  of the original trajectory (i.e., every patch  $i$  is occupied at its carrying capacity  $K_i$  at this limit point). Because the origin is a repeller for Eq. 4, it is not contained in any  $\omega$ -limit set. As the set of  $\omega$ -limit points consists of fixed points and the arcs of trajectories connecting them (Hartman 1964), we conclude that all trajectories of Eq. 4 converge to  $(x^*, \tilde{x}^*)$ .

## Appendix 2

First, we derive model 7. The resident fitness

$$W(u, u; x) = u_1 r_1 \left( 1 - \frac{u_1 x}{K_1} \right) + u_2 r_2 \left( 1 - \frac{u_2 x}{K_2} \right)$$

gives the per capita population growth rate. At low population density (i.e.,  $x < K_1(r_1 - r_2)/r_1$ ) all individuals should occupy patch 1 ( $u_1 = 1$  and  $u_2 = 0$ ) and we get the first part of model 7. At higher population densities, we know that both patches provide the same payoff  $\left( r_1 \left( 1 - \frac{u_1 x}{K_1} \right) = r_2 \left( 1 - \frac{u_2 x}{K_2} \right) \right)$  and so the resident fitness simplifies to

$$W(u, u; x) = r_1 \left( 1 - \frac{u_1 x}{K_1} \right)$$

Substitution of Eq. (6) into  $W$  yields

$$\begin{aligned} W(u, u; x) &= r_1 \left( 1 - \frac{r_2 x}{r_2 K_1 + r_1 K_2} - \frac{K_2 (r_1 - r_2)}{r_2 K_1 + r_1 K_2} \right) \\ &= \frac{r_1 r_2 x}{K_2 r_1 + K_1 r_2} (K_1 + K_2 - x) \end{aligned}$$

Second, we derive model 8. The resident population dynamics are

$$\begin{aligned} \frac{dx}{dt} &= xW(u, u; \tilde{u}, x, \tilde{x}) = x \left\langle u, A(x, \tilde{x}, \tilde{u}) u \right\rangle \\ &= x u_1 \left( r_1 u_1 \left( 1 - \frac{x + \tilde{u}_1 \tilde{x}}{K_1} \right) + r_1 u_2 \left( 1 - \frac{\tilde{u}_1 \tilde{x}}{K_1} \right) \right) \\ &\quad + x u_2 \left( r_2 u_1 \left( 1 - \frac{\tilde{u}_2 \tilde{x}}{K_2} \right) + r_2 u_2 \left( 1 - \frac{x + \tilde{u}_2 \tilde{x}}{K_2} \right) \right) \\ &= x \left( r_1 u_1 + r_2 u_2 - x \left( \frac{r_1 u_1^2}{K_1} + \frac{r_2 u_2^2}{K_2} \right) - \frac{K_2 r_1 u_1 \tilde{u}_1 + K_1 r_2 u_2 \tilde{u}_2}{K_1 K_2} \tilde{x} \right) \\ &= (r_1 u_1 + r_2 u_2) x \left( 1 - \frac{x}{k_1} - \frac{\alpha}{k_1} \tilde{x} \right) \end{aligned}$$

where

$$k_1 = \frac{K_1 K_2 (r_1 u_1 + r_2 u_2)}{K_2 r_1 u_1^2 + K_1 r_2 u_2^2} \text{ and } \alpha = \frac{K_2 r_1 u_1 \tilde{u}_1 + K_1 r_2 u_2 \tilde{u}_2}{K_2 r_1 u_1^2 + K_1 r_2 u_2^2}$$

Derivation of the mutant population dynamics in (8) is analogous.

It is important to note that interior equilibrium

$$E = \left( \frac{K_1 - (K_1 + K_2) \tilde{u}_1}{u_1 - \tilde{u}_1}, \frac{(K_1 + K_2) u_1 - K_1}{u_1 - \tilde{u}_1} \right)$$

of model 8 is positive if residents and mutants have fixed strategies that show distinct preferences for the two patches with respect to carrying capacities, which can be written as  $(u_1 - K_1/(K_1 + K_2))(\tilde{u}_1 - K_1/(K_1 + K_2)) < 0$ . In fact, this equilibrium is always stable. Indeed, the stability condition for the Lotka-Volterra competitive system (Eq. 8)

$$\alpha\beta = \frac{(K_2r_1u_1\tilde{u}_1 + K_1r_2u_2\tilde{u}_2)^2}{(K_2r_1u_1^2 + K_1r_2u_2^2)(K_2r_1\tilde{u}_1^2 + K_1r_2\tilde{u}_2^2)} < 1$$

simplifies to

$$-K_1K_2r_1r_2(\tilde{u}_1 - u_1)^2 < 0$$

which is always true (provided we assume mutants and residents use different strategies,  $\tilde{u}_1 \neq u_1$ ).

Now, let us consider the situation where residents and mutants show preference for the same patch, i.e.  $(u_1 - K_1/(K_1 + K_2))(\tilde{u}_1 - K_1/(K_1 + K_2)) > 0$ . In this case no interior equilibrium exists and one population will outcompete the other population. Here we show that the population with strategy that brings the population distribution closer to the IFD will survive while the other will die out. This depends on the position of resident and mutant isoclines. Under the assumption of the same preferences, these two isoclines do not intersect in the positive quadrant and the mutant isocline will be below the resident isocline when  $k_2/\beta < k_1$ . In this case, the resident population will survive and outcompete mutants. This inequality is equivalent to

$$\left(\frac{K_1}{K_1 + K_2} - u_1\right)(u_1 - \tilde{u}_1) > 0$$

To satisfy this inequality there are two possibilities: Either residents show preference for patch 2  $\left(u_1 < \frac{K_1}{K_1 + K_2}\right)$

and  $u_1 > \tilde{u}_1$ , or residents show preference for patch 1  $\left(u_1 > \frac{K_1}{K_1 + K_2}\right)$  and  $u_1 < \tilde{u}_1$ . In both cases, the resident strategy matches the IFD better than the mutant strategy does. Similarly, if the mutant strategy matches the IFD better than the resident strategy does, mutants will replace residents.

### Appendix 3

For the logistic model, we also claim that mutants persist after they are introduced into the resident-mutant system at a positive factor  $k^*$  of the population. From models 10 and 11, we have that, for  $0 < x < x^1$ ,  $\frac{d(\tilde{x}/x)}{dt} \leq 0$  with equality if and only if  $\tilde{u}_1 = 1$ . Similarly, for  $0 < x < x^2$ ,  $\frac{d(\tilde{x}/x)}{dt} \leq 0$  with equality if and only if  $\tilde{u}_1 = 0$ . Finally, if  $x \geq \max\{x^1, x^2\}$ ,  $\frac{d(\tilde{x}/x)}{dt} = 0$ . In particular  $\frac{\tilde{x}(t)}{x(t)} \leq \frac{\tilde{x}(0)}{x(0)}$  for all  $t \geq 0$ .

From these results, if  $\tilde{x}(t_0)$  is small enough and  $x(t_0)$  is close to the equilibrium population density  $K_1 + K_2$ , then  $x > \max\{x^1, x^2\}$  for all  $t \geq t_0$  and for any choice of  $\tilde{u}$ . Thus  $\frac{d(\tilde{x}/x)}{dt} = 0$  for  $t \geq t_0$ . That is,  $\tilde{x}/x$  will remain constant (and positive) for  $t$  sufficiently large (i.e.  $t > t_0$ ) along any trajectory and so the mutants do not die out entirely. Furthermore,  $\frac{d(x + \tilde{x})}{dt} > 0$  (respectively,  $\frac{d(x + \tilde{x})}{dt} > 0$ ) if  $x + \tilde{x} < K_1 + K_2$  (respectively,  $x + \tilde{x} > K_1 + K_2$ ) for  $t \geq t_0$  and so  $x + \tilde{x}$  converges to  $K_1 + K_2$ .