

# Habitat Selection by Two Competing Species in a Two-Habitat Environment

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Submitted April 23, 2001; Accepted January 10, 2002

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**ABSTRACT:** We present a theoretical study of habitat selection strategies for two species that compete in an environment consisting of two different habitats. Our fitness functions are derived from the Lotka-Volterra competition equations, and we assume that individuals settle in the habitat in which their fitness is maximized. We derive an ideal free distribution across the habitats for both species. Our model provides analytical and graphical descriptions of individual habitat selection behavior, isolegs (the boundary lines separating regions where qualitatively different habitat preferences are predicted), and spatial population distributions. Our analysis reveals complex isolegs, several novel patterns of habitat distribution, and even situations where spatial strategies, as well as the relative abundances of coexisting species, exhibit only local stability. Hence, distributions of competing species may be determined not solely by their respective densities but also by the order of colonization. This happens, however, only for extreme levels of interspecific competition. In the situation where one competitor species is dominant over the other, our model predicts isolegs that qualitatively agree with observed behavioral patterns. However, our model predicts a greater variety of possible situations than has been previously described. Finally, we analyze the influence of habitat selection behavior on species isoclines and verify that increasing interspecific competition leads to habitat segregation.

*Keywords:* density dependence, habitat selection, ideal free distribution, interspecific competition, isoclines, isolegs.

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Strategies for habitat selection have a strong influence on individual success because abundance and accessibility of resources are discontinuous in natural environments. In addition, variations in habitat quality influence local aggregations and dispersal of both intraspecific and interspecific competitors (Werner and Hall 1979; M'Closkey 1981; Pierotti 1982; Bowers et al. 1987; Aho et al. 1997; Robinson and Sutherland 1999). That is why individual habitat selection behavior is influenced by resource availability and density of competitors and why individual behavior and populations interactions are tightly coupled (Hairston 1980; Ives 1988; Morris 1988; Brown and Pavlovic 1992; Wilson and Yoshimura 1994; Rosenzweig 1995; Sutherland 1996; Rosenzweig and Abramsky 1997).

In this article, we focus on two species that are competing for resources in a heterogeneous environment consisting of two different habitats (Pulliam and Mills 1977; Werner and Hall 1979; Howard and Harrison 1984; Pimm et al. 1985; Brown 1988; Abramsky and Pinshow 1989; Abramsky et al. 1990; Dooley and Dueser 1996; Morris et al. 2000). Our model predicts how each species should be distributed across the habitats; it assumes that each individual selects its habitat in an adaptive way, as a response to environmental heterogeneity and competition imposed by conspecific and heterospecific animals. To model the effects of intra- and interspecific competition on individual success, we assume that individual fitness linearly decreases with increasing densities of intra- and interspecific competitors (Pimm and Rosenzweig 1981). We assume that both species are distributed across habitats so that no individual can increase its fitness by changing habitat choice and that this distribution is stable with respect to small spatial disturbances. Such a distribution is a generalization of the classic ideal free distribution (IFD) for a single population (Fretwell and Lucas 1970; Rosenzweig 1981). While derivation of IFD for a single population is a straightforward task, it is more complicated for two or more species because the distribution of one species influences the distribution of the other species, which, in turn, affects the distribution of the first species. Thus, simultaneous derivation of IFD for two species requires a

game theoretical approach (Maynard Smith 1982; Thomas 1986; Hofbauer and Sigmund 1998).

We represent these distributions graphically in the population-density phase space by plotting isolegs, which are the lines separating regions where qualitatively different habitat preferences are observed (Rosenzweig 1979, 1981, 1991). In the literature, the shape of isolegs is often assumed to have some a priori functional form (linear, piecewise linear, or nonlinear) that is then fitted to existing data (Rosenzweig 1986; Rosenzweig and Abramsky 1986; Abramsky et al. 1990). In contrast, we derive functional shape of isolegs from the assumption that both species follow IFD across the habitats.

We study both the situation in which both species show initial preference for the same part of the environment (Abramsky et al. 1990; Ziv et al. 1995) and the situation in which both species prefer different habitats (Morris 1996; Morris et al. 2000). We also explore the situation in which one species is dominant over the other, and this has been extensively studied in the field (Lawton and Hassell 1981; Connell 1983; Schoener 1983; Morin and Johnson 1987).

Our analytical approach allows us to determine precisely the shape and position of isolegs and to discuss in more detail the effect of competition on habitat selection. We show that it may not be possible to predict a unique IFD for each set of species densities when interspecific competition is strong compared to intraspecific competition. In this case, isolegs are not well defined in certain regions of species-density phase space. Thus, in highly competitive situations, the actual distribution of both species will depend on the order of species arrivals.

Our objective is to predict distribution of each species in each habitat without necessarily assuming that population densities settle at an equilibrium. This is because individuals are likely to experience a wide range of densities in the field, as a result of, for example, accidental or seasonal changes (Pimm et al. 1985) or migration (Terrill 1990). However, it is also important to examine the effects of habitat selection strategies on the dynamics of the community (Pimm and Rosenzweig 1981; Morris et al. 2000). In our study, we evaluate Lotka-Volterra population dynamics for two competing species in a two-habitat environment, and we assume that species are distributed according to the IFD. We show that adaptive habitat choice leads to piecewise linear isoclines and that habitat segregation occurs when interspecific competition exceeds a certain threshold.

### Distribution of a Single Population

First, we consider a single population living in an environment consisting of two spatially segregated habitats

with specific demographic parameters ( $r_{N_1}$  and  $K_{N_1}$  for habitat 1 and  $r_{N_2}$  and  $K_{N_2}$  for habitat 2, respectively). Here  $r$  stands for the per capita intrinsic population growth rate and  $K$  for the carrying capacity of the habitat. Following Fretwell and Lucas (1970), we assume that animals move freely from habitat to habitat instantaneously and without cost.

Let  $N_1$  and  $N_2$  be the population densities in habitats 1 and 2, respectively, and  $n$  and  $1 - n$  be the respective proportions of animals in habitat 1 and 2. Then  $N_1 = nN$  and  $N_2 = (1 - n)N$ , where  $N$  denotes the overall population density. Note that  $n$  reflects the preference of an average animal for habitat 1. Habitat preference ( $n$ ) has two interpretations. At the individual level, it is the proportion of time that an average animal spends in habitat 1. At the population level, it is the proportion of the total population making use of habitat 1. Thus, at the individual level, habitat preference ( $n$ ) represents the individual strategy for habitat selection. In this model, we make no assumption concerning the level of spatial heterogeneity. Thus, our derivations apply to particular environments in which there are two habitats or resource patches that are segregated spatially. But our conception can be extended to environments in which two habitat types are spatially juxtaposed over the landscape as a mosaic of habitats. However, in fine-grained environments, it may be practically impossible for animals to visit one type of habitat only (Morris 1999). Following Fretwell and Lucas (1970), we require IFD to satisfy two conditions: (1) no individual can unilaterally increase its fitness by changing its strategy, i.e., by changing its habitat preferences, and (2) the spatial distribution is stable against small fluctuations in the spatial species distribution. Thus, in our setting, IFD is nothing other than the Nash equilibrium (Thomas 1986; Hofbauer and Sigmund 1998). In the framework of game theory, condition 2 is the “stability condition” that describes stability of the Nash equilibrium against fluctuations in the spatial species distribution. We remark that for a single population, the two conditions are those that define evolutionarily stable strategy (Hofbauer and Sigmund 1998).

We assume that fitness is measured by the per capita growth rate of the population. Individual success is then a function of overall population density ( $N$ ) and individual strategy ( $n$ ). If we assume that population growth is logistic, fitness of an individual in habitat 1 is

$$W_1(n, N) = \frac{dN_1/dt}{N_1} = r_{N_1} \left( 1 - \frac{nN}{K_{N_1}} \right),$$

and in habitat 2,

$$W_2(n, N) = \frac{dN_2/dt}{N_2} = r_{N_2} \left( 1 - \frac{(1-n)N}{K_{N_2}} \right).$$

We assume, without loss of generality, that the intrinsic per capita growth rate in habitat 1 is higher than in habitat 2 ( $r_{N_1} > r_{N_2}$ ). This means that at low densities, when intraspecific competition is weak, individual success is higher in habitat 1 than in habitat 2. Following Morris (1988), we will say that habitat 1 is quantitatively better than habitat 2, for example, because resource standing crop is higher there. Hence, at low population densities, only habitat 1 will be colonized ( $n = 1$ ; fig. 1). When population density is high, a high level of competition in habitat 1 can make this habitat less profitable than habitat 2. So when density exceeds a certain threshold, it pays for an animal to share its time between habitat 1 and the poorer, but less crowded, habitat 2. The density threshold  $N^*$ , where animals should switch from specialist to generalist behavior, satisfies

$$W_1(1, N^*) = W_2(1, N^*),$$

which gives the minimal overall population density above which both habitats are occupied

$$N^* = \frac{K_{N_1}(r_{N_1} - r_{N_2})}{r_{N_1}}. \tag{1}$$

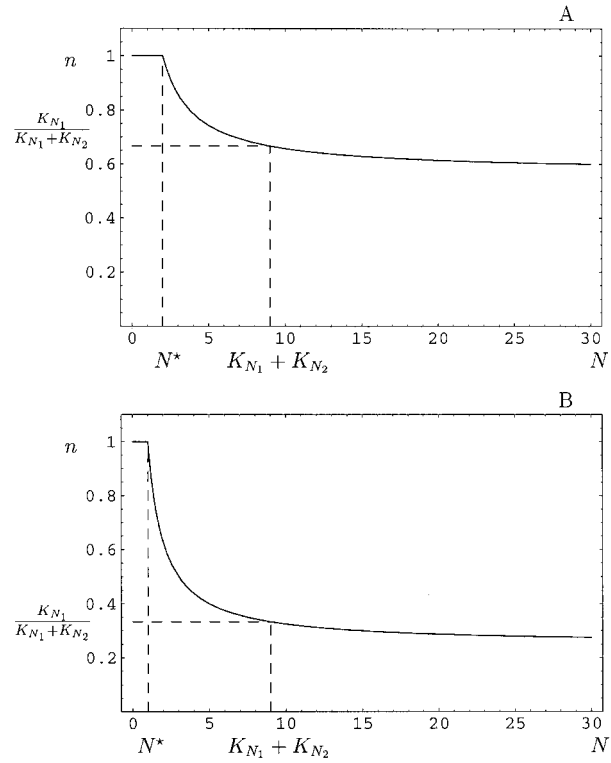
Since  $N^* < K_{N_1}$ , animals will begin to colonize habitat 2 before the carrying capacity in habitat 1 is reached, and colonization starts sooner when the difference between habitat intrinsic growth rate parameters is smaller. When population density ( $N$ ) exceeds the switching threshold ( $N^*$ ), IFD theory tells us that animals should share their time between habitats 1 and 2 in such a way that fitness remains the same in both habitats, that is,

$$W_1(n, N) = W_2(n, N),$$

which yields animal distribution in habitat 1:

$$n = \frac{r_{N_2}K_{N_1}}{r_{N_2}K_{N_1} + r_{N_1}K_{N_2}} + \frac{K_{N_1}K_{N_2}(r_{N_1} - r_{N_2})}{(r_{N_2}K_{N_1} + r_{N_1}K_{N_2})N}. \tag{2}$$

In figure 1, IFD ( $n$ ) is plotted as a function of overall population density ( $N$ ). Figure 1 shows that, above the switching threshold  $N^*$ , the proportion of animals in habitat 1 is a decreasing function of the overall population density. These computations allow us to derive for our system a rule analogous to the input-matching rule (Parker 1978; Sutherland 1996) that relates the ratio of resource input rates to the ratio of consumers in corresponding



**Figure 1:** Ideal free distribution (IFD) of a single population as a function of its overall density  $N$ . Preference  $n$  for habitat 1 represents the proportion of the population in this habitat. Values of  $N = K_{N_1} + K_{N_2}$  and  $n = K_{N_1}/(K_{N_1} + K_{N_2})$  correspond to the population equilibrium density. *A* assumes that habitat 1 is qualitatively better than habitat 2 ( $r_{N_1}/K_{N_1} < r_{N_2}/K_{N_2}$ ), in which case habitat 1 is the preferred habitat at high population densities. *B* assumes that habitat 2 is qualitatively better than habitat 1 ( $r_{N_1}/K_{N_1} > r_{N_2}/K_{N_2}$ ), in which case the preference for habitat 1 at low population densities ( $r_{N_1} > r_{N_2}$ ) switches to preference for habitat 2 at high densities. Parameters in *A*:  $r_{N_1} = 3$ ,  $r_{N_2} = 2$ ,  $K_{N_1} = 6$ ,  $K_{N_2} = 3$ . Parameters in *B*:  $r_{N_1} = 3$ ,  $r_{N_2} = 2$ ,  $K_{N_1} = 3$ ,  $K_{N_2} = 6$ .

habitats. This rule was originally derived for “continuous systems” in which resources are immediately consumed upon arrival (Parker and Stuart 1976; Parker 1978; Milinski and Parker 1991) and extended to the case of nonzero standing crop (Lessells 1995; V. Křivan, unpublished manuscript). Our model does not explicitly incorporate resource dynamics because resources are treated as a component of the environment reflected by model parameter values. Thus, habitat value depends solely on these parameters and the number of competitors present. The corresponding matching rule is given by

$$\frac{n}{1-n} = \frac{K_{N_1}[K_{N_2}(r_{N_1} - r_{N_2}) + r_{N_2}N]}{K_{N_2}[K_{N_1}(r_{N_2} - r_{N_1}) + r_{N_1}N]}. \tag{3}$$

As population density  $N$  reaches high values, resources

will be consumed more quickly, and the matching rule simplifies approximately to

$$\frac{n}{1-n} \approx \frac{r_{N_2}/K_{N_2}}{r_{N_1}/K_{N_1}}. \quad (4)$$

The ratio  $-r_{N_i}/K_{N_i}$  is the slope (with respect to animal abundance) of the fitness function in habitat  $i$  ( $i = 1, 2$ ). Hence, the habitat with the smallest  $r/K$  value is the one where the per capita effect of competition is weakest. Formula (4) predicts that it will be preferred at high consumer densities; that is, the proportion of population in this habitat will be higher than that in the other habitat. Qualitatively, there are two possibilities: either  $r_{N_1}/K_{N_1} < r_{N_2}/K_{N_2}$  and then habitat 1 will be preferred at both low and high densities (fig. 1A) or  $r_{N_1}/K_{N_1} > r_{N_2}/K_{N_2}$  and then habitat preferences will switch from habitat 1 at low densities to habitat 2 at high densities (fig. 1B). This is because the originally more productive habitat 1 is more strongly depreciated at high densities of consumers, for example, because of lower renewal rate of resources (Holt 1985; Morris 1988). These different modes of population regulation were considered by Morris (1988). Following Morris, we say that habitats differ quantitatively if they have different  $r_{N_i}$  values and qualitatively if they have different  $r_{N_i}/K_{N_i}$  values. These conclusions have an important bearing for the case of two competing populations, as we will see.

### Consequences for Population Dynamics of a Single Species

Here we consider the dynamics of an isolated population, still assuming that animals disperse across habitats 1 and 2 according to the IFD, as described above. Assuming that animals migrate fast enough between habitats and that population growth in either habitat is logistic, corresponding overall population dynamics are

$$\frac{dN}{dt} = r_{N_1}nN\left(1 - \frac{nN}{K_{N_1}}\right) + r_{N_2}(1-n)N\left(1 - \frac{(1-n)N}{K_{N_2}}\right).$$

Below the threshold ( $N^*$ ), animals prefer habitat 1, and population dynamics are described by the above differential equation, where we set  $n = 1$ . Above the threshold, animals use both habitats, and population dynamics are described by the above model, where we set  $n$  given by formula (2). Thus, overall population dynamics are described by a piecewise logistic equation:

$$\frac{dN}{dt} = \begin{cases} r_{N_1}N\left(1 - \frac{N}{K_{N_1}}\right) & \text{if } N < N^* \\ \frac{r_{N_1}r_{N_2}N}{K_{N_2}r_{N_1} + K_{N_1}r_{N_2}}(K_{N_1} + K_{N_2} - N) & \text{if } N \geq N^*. \end{cases} \quad (5)$$

For any given initial population density, the total population reaches equilibrium abundance,  $K_{N_1} + K_{N_2}$ , at which the population density in either habitat equals the carrying capacity of that habitat. The matching principle (3) evaluated at the equilibrium states that

$$\frac{n}{1-n} = \frac{K_{N_1}}{K_{N_2}}.$$

### Distribution of Two Competing Species

Now we consider two different species, with total abundances  $N$  and  $P$ , respectively, in a two-habitat environment. We have  $N = N_1 + N_2$  and  $P = P_1 + P_2$ , where  $N_i$  and  $P_i$  are the respective abundances of species  $N$  and  $P$  in habitat 1. Following the model given for a single population, we assume that individual fitness decreases linearly with increasing densities of both conspecific and hetero-specific competitors.

Interspecific competition is described by competition coefficients  $\alpha$  and  $\beta$ , which model the effect of the second species on the first species and of the first species on the second species, respectively. If  $n$  and  $1-n$  are the proportions of species  $N$  in habitat 1 and habitat 2, and  $p$  and  $1-p$  are the proportions of species  $P$  in habitat 1 and habitat 2, respectively, then animal fitness in either habitat is

$$W_{N_1}(n, p; N, P) = r_{N_1}\left(1 - \frac{nN}{K_{N_1}} - \frac{\alpha pP}{K_{N_1}}\right),$$

$$W_{N_2}(n, p; N, P) = r_{N_2}\left(1 - \frac{(1-n)N}{K_{N_2}} - \frac{\alpha(1-p)P}{K_{N_2}}\right),$$

$$W_{P_1}(n, p; N, P) = r_{P_1}\left(1 - \frac{pP}{K_{P_1}} - \frac{\beta nN}{K_{P_1}}\right),$$

$$W_{P_2}(n, p; N, P) = r_{P_2}\left(1 - \frac{(1-p)P}{K_{P_2}} - \frac{\beta(1-n)N}{K_{P_2}}\right)$$

(here and in what follows, the first subindex refers to population while the second denotes the habitat). Thus,  $W_{ij}(n, p; N, P)$  is the fitness for individuals belonging to species  $i$  ( $i = N, P$ ) in habitat  $j$  ( $j = 1, 2$ ) for population

distributions  $n$  and  $p$  and overall population densities  $N$  and  $P$ . Fitness of an animal now depends not only on the distribution of its own population but also on the distribution of the other population. Without loss of generality, we assume that at low species densities the first habitat is better for the first population than the second habitat, which means that  $r_{N_1} > r_{N_2}$ .

Now we derive joint IFD for the two species. Because we defined IFD as the Nash equilibrium, we can follow standard methodology for computation of Nash equilibria (Thomas 1986). A method for computing this is to describe the single IFD of the first species for any distribution of the second species and conversely. The intersection of these two curves in species distribution space defines the possible candidates for joint IFD (Thomas 1986). We do this now. For a fixed strategy  $p$  of the second species, the strategy of the first species is to distribute across habitats in such a way that no individual of this species can increase its fitness by moving to the other habitat. As we saw earlier, this means that either all individuals of the first species are in the habitat that provides them with a higher per capita growth rate (habitat 1) or the population distributes across the two habitats in such a way that per capita growth rate in both habitats is the same, that is,

$$W_{N_1}(n, p; N, P) = W_{N_2}(n, p; N, P). \quad (6)$$

This allows us to compute IFD of the first species  $n(p)$  for every distribution  $p$  of the second species (*solid line*, fig. 2 and app. A). Similarly, we compute IFD of the second species  $p(n)$  for each possible distribution  $n$  of the first species (*dashed line*, fig. 2 and app. A).

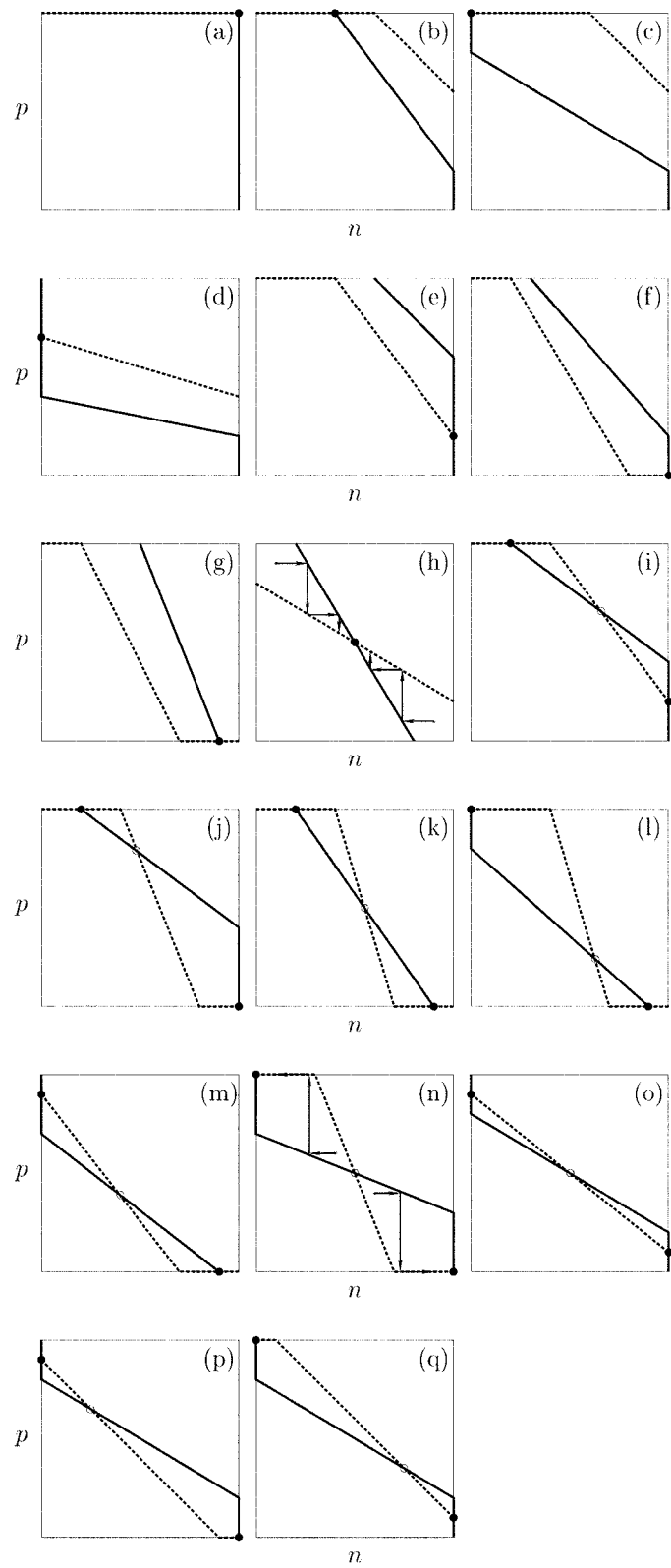
These curves intersect generically either at one or at three points (fig. 2). Qualitatively, there are two possibilities. Either there is no interior intersection point, and in this case there is only one IFD, for which one or both species specialize in one habitat only (fig. 2*a*–2*g*), or an interior intersection point exists, which we denote by  $(n^*, p^*)$ . In the latter case, there may be two boundary intersection points (fig. 2*i*–2*q*) or no boundary intersection point (fig. 2*h*). For complete classification of all possibilities listed in figure 2, see appendix A. Some of the intersection points are unstable with respect to small fluctuations in the spatial distribution, as is graphically demonstrated in figure 2*n*. These unstable equilibria are denoted by open circles (fig. 2*i*–2*q*). In other words, such distributions are ecologically implausible because they are not persistent with respect to accidental changes in species spatial distributions. Thus, only those intersection points that are stable with regard to small spatial perturbations define IFDs.

We remark that the interior intersection point is an IFD (i.e., stable) provided that at this point the slope of the

solid line (that describes strategies of the first species;  $-N/[\alpha P]$ ) is smaller than is the slope of the dashed line (that describes strategies of the second species;  $-\beta N/P$ ; see case *h* of fig. 2 and app. A). Therefore, a necessary condition for the interior intersection point to be an IFD is  $\alpha\beta < 1$ , which represents weak interspecific competition. If the opposite inequality holds, then the interior intersection point cannot be an IFD because it is unstable with respect to small spatial perturbations. In this case, no IFD would keep the two species distributed across both habitats.

If there are two IFDs, we may ask which one will be chosen, realistically. Consider the case of colonization of two empty habitats by two species. The species that arrives first will split across the two habitats, following the rules for a single population. When the second population arrives, both populations will redistribute to a new IFD that is now uniquely determined by the distribution of the first population. We call this situation the “priority effect” because the resulting IFD depends on the distribution of the population that arrived first. For example, consider the situation depicted in figure 2*n*, and assume that population  $N$  arrived before population  $P$ . Depending on its total abundance, population  $N$  will distribute across the two habitats following strategy described by equation (2). Following this distribution, the corresponding IFD when the second species is introduced is either (1, 0) or (0, 1) (fig. 2*n*). Thus, without knowing “who arrived first,” we cannot uniquely determine the corresponding IFD.

In appendix A we expose how possible distributions are derived for all sets of population densities  $(N, P)$ . The map that associates the corresponding IFD to species density  $(N, P)$  is called the habitat selection graph (Abramsky et al. 1990). As discussed above, this graph, or map, may be multivalued; that is, for certain population densities there are two possible spatial distributions. For each species and for each set of population densities there are the following three possible IFDs: first,  $n$  (or  $p$ ) = 0 and the species visits only habitat 2; second,  $0 < n$  (or  $p$ ) < 1 and the species visits both habitats; and third,  $n$  (or  $p$ ) = 1 and the species visits only habitat 1. The curves that separate the above three regions are called isolegs (Rosenzweig 1979, 1981, 1986, 1991; Pimm et al. 1985). For each species there are two isolegs. For the  $N$  species, the first isoleg, which delimits the part of the space in which it specializes in habitat 1, is called 0% isoleg, and we denote it as  $N_1^*$  (*solid line*, figs. 3–5). The second isoleg, which delimits specialization in habitat 2, is called 100% isoleg, and we denote it as  $N_2^*$  (*long dashed line*, figs. 3, 4). In the region between these two isolegs, species  $N$  visits both habitats. Similarly, for  $P$  species we have 0% and 100% isolegs denoted as  $P_1^*$  (*dashed line*, figs. 3–5) and  $P_2^*$  (*dotted line*, figs. 3–5), respectively.



Here we briefly survey general properties of isolegs for our model. All isolegs are piecewise straight lines, and their respective position depends on the values of the parameters. Our analysis shows that, theoretically, isolegs cannot be uniquely defined due to the multivaluedness of the habitat selection map. However, this can happen only provided the relative strength of the interspecific competition with respect to intraspecific competition is very strong (i.e.,  $\alpha\beta > 1$ ). In this case, nonuniqueness in the strategy only concerns certain regions of the density space (those bounded by the solid quadrangle in figs. 3E, 4E) where two alternative distributions are predicted. The Mathematica III notebook that draws the habitat selection map is available from the author on request. Here we graphically analyze habitat selection maps along a gradient (described by parameter  $\sigma$ ) that measures the strength of intraspecific competition relative to that of interspecific competition. Fitness functions are then

$$\begin{aligned}
 W_{N_1}(n, p; N, P) &= r_{N_1} \left( 1 - \frac{n\sigma N}{K_{N_1}} - \frac{\alpha' p(1 - \sigma)P}{K_{N_1}} \right), \\
 W_{N_2}(n, p; N, P) &= r_{N_2} \left( 1 - \frac{(1 - n)\sigma N}{K_{N_2}} \right. \\
 &\quad \left. - \frac{\alpha'(1 - p)(1 - \sigma)P}{K_{N_2}} \right), \\
 W_{P_1}(n, p; N, P) &= r_{P_1} \left( 1 - \frac{p\sigma P}{K_{P_1}} - \frac{\beta' n(1 - \sigma)N}{K_{P_1}} \right), \quad (7) \\
 W_{P_2}(n, p; N, P) &= r_{P_2} \left( 1 - \frac{(1 - p)\sigma P}{K_{P_2}} \right. \\
 &\quad \left. - \frac{\beta'(1 - n)(1 - \sigma)N}{K_{P_2}} \right).
 \end{aligned}$$

For  $\sigma = 0$ , fitness functions given by equation (7) describe a system with interspecific competition only, while for  $\sigma = 1$ , they describe a system with intraspecific competition only. In what follows we will analyze graphically the positions of isolegs with respect to decreasing values of parameter  $\sigma$  (figs. 3, 4). By doing so, we progressively

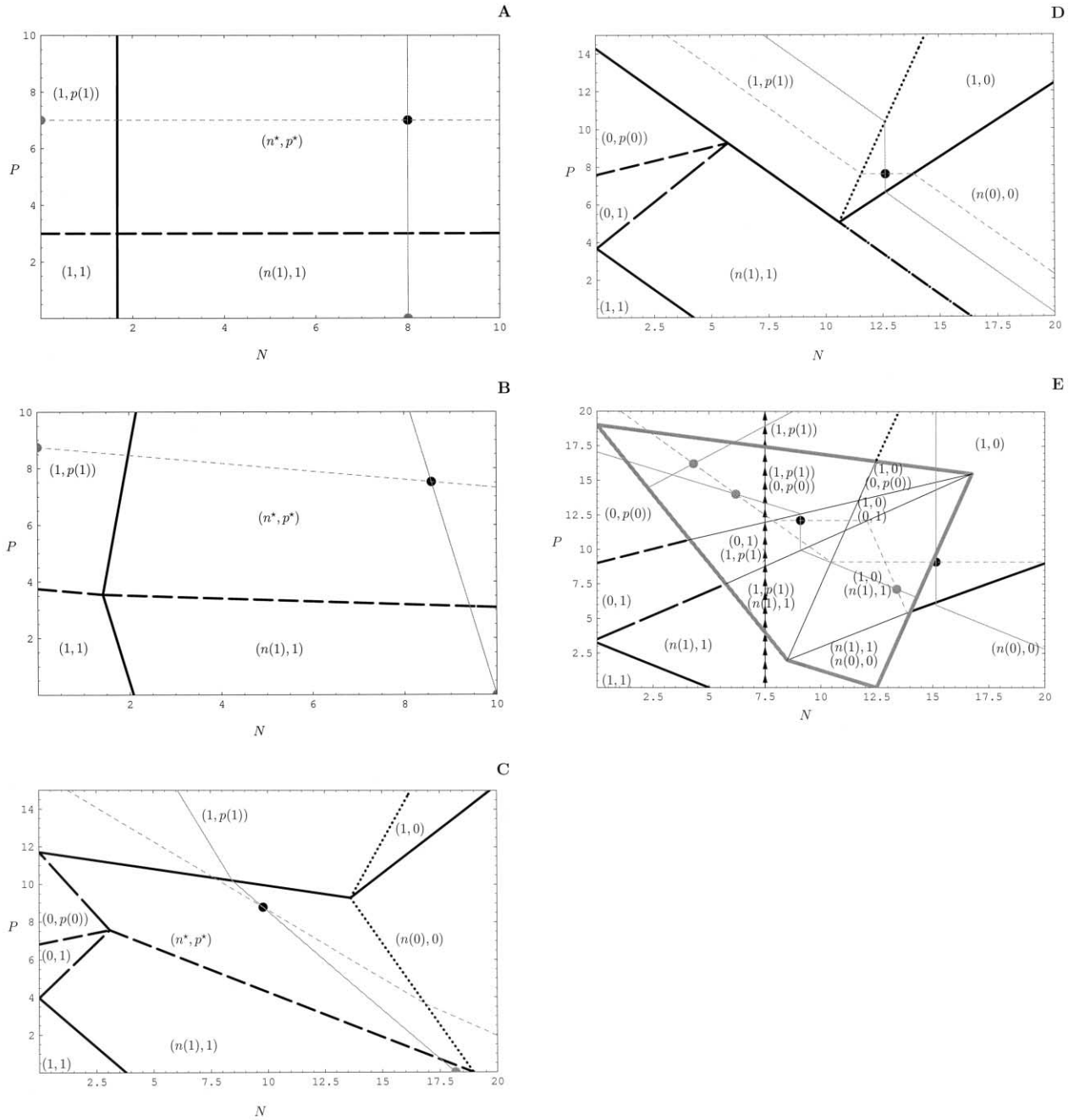
increase the relative level of interspecific competition, and we evaluate its effect on individual habitat selection behavior. The numbers given in figures 3 and 4 describe the joint species IFD. Each couple of numbers describes proportion of species  $N$  and  $P$  in habitat 1. Values for  $p(0)$ ,  $p(1)$ ,  $n(0)$ ,  $n(1)$ ,  $n^*$ , and  $p^*$  are given explicitly in appendix A.

### The Shared-Preference Case

Here we consider the case in which both species prefer the same habitat at low density, which happens when the growth rate parameters for both species are higher in the same habitat ( $r_{N_1} > r_{N_2}$  and  $r_{P_1} > r_{P_2}$ ). When only intraspecific competition is considered ( $\sigma = 1$ ; fig. 3A), the two species do not interact, and each of them distributes following the rules given for a single isolated population. Thus, we observe only 0% isolegs  $N_1^*$  and  $P_1^*$  because neither of the two species ever occupies exclusively the poorer habitat 2, as we showed for the single species case. Isolegs are straight perpendicular lines. As  $\sigma$  decreases from 1, interspecific competition increases, and isolegs  $N_1^*$  and  $P_1^*$  become piecewise linear lines with sharp angles at the intersection point (fig. 3B). The fact that isolegs change direction when crossing each other is an important and ubiquitous prediction of our model. The reason is that when one species qualitatively changes its distribution (e.g., from inhabiting only one habitat to inhabiting both habitats or vice versa), the other species must redistribute too. This is reflected in the change of the slope of its isoleg. Consider, for example, the case described in figure 3B. Isoleg  $N_1^*$  (*solid line*) gives us, for each possible density of species  $P$ , the density threshold above which members of species  $N$  choose to spend some time in the poor part of their environment (i.e., habitat 2). Below their own 0% isoleg  $P_1^*$  (*dashed line*), members of species  $P$  visit only habitat 1. As density  $P$  increases, the suitability of habitat 1 decreases for animals of species  $N$ , and so this species will begin to visit habitat 2 at lower intraspecific densities (see the orientation of isoleg  $N_1^*$  in fig. 3B below the dashed line). Above their own isoleg  $P_1^*$ , animals of species  $P$  visit both habitats, more equally distributing interspecific competition among habitat 1 and 2 for species  $N$ . In other words, interspecific competition now increases more

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**Figure 2:** Graphical approach for computation of joint IFD for two competing species. Here  $n(p)$  (*solid line*) is the IFD of species  $N$  for each possible distribution  $p$  of species  $P$ , and  $p(n)$  (*dashed line*) is the IFD of species  $P$  for each distribution  $n$  of species  $N$ . The intersections of these two piecewise linear lines define those strategies for both species that are optimal in the sense that no other strategy can achieve unilaterally higher fitness in this population. The equilibrium points denoted by open circles are unstable with respect to small changes in population densities. Those denoted by filled circles are stable, and they define IFD.  $a$ - $q$  correspond to all qualitative cases for IFD positions that are listed in appendix A.



**Figure 3:** Habitat selection maps for the shared-preference case. 0% (*heavy solid line*) and 100% (*heavy long-dashed line*) isolegs for species  $N$  and 0% (*heavy dashed line*) and 100% (*heavy dotted line*) isolegs for species  $P$  separate regions with qualitatively different species distributions. Proportions of species  $N$  and  $P$  in first habitat are given in parentheses for each region. In *A* the strength of intraspecific competition relative to the interspecific competition is high ( $\sigma = 1$ ), and it decreases subsequently:  $\sigma = 0.8$  in *B*;  $\sigma = 0.44$  in *C*;  $\sigma = 0.396$  in *D*;  $\sigma = 0.33$  in *E*. In the region bounded by the heavy gray quadrangle in *E*, IFD is not uniquely defined and, consequently, isolegs also cannot be defined. Gray lines are isoclines (solid line is the isocline for the first species; dashed line is the isocline for the second species). Locally stable equilibria are denoted by filled circles; unstable equilibria are denoted by gray circles. Parameters:  $\alpha = 3/4(1 - \sigma)/\sigma$ ,  $\beta = 4/7(1 - \sigma)/\sigma$ ,  $K_{N_1} = 5/\sigma$ ,  $K_{N_2} = 3/\sigma$ ,  $K_{P_1} = 4/\sigma$ ,  $K_{P_2} = 3/\sigma$ ,  $r_{N_1} = 3$ ,  $r_{N_2} = 2$ ,  $r_{P_1} = 4$ ,  $r_{P_2} = 1$ .



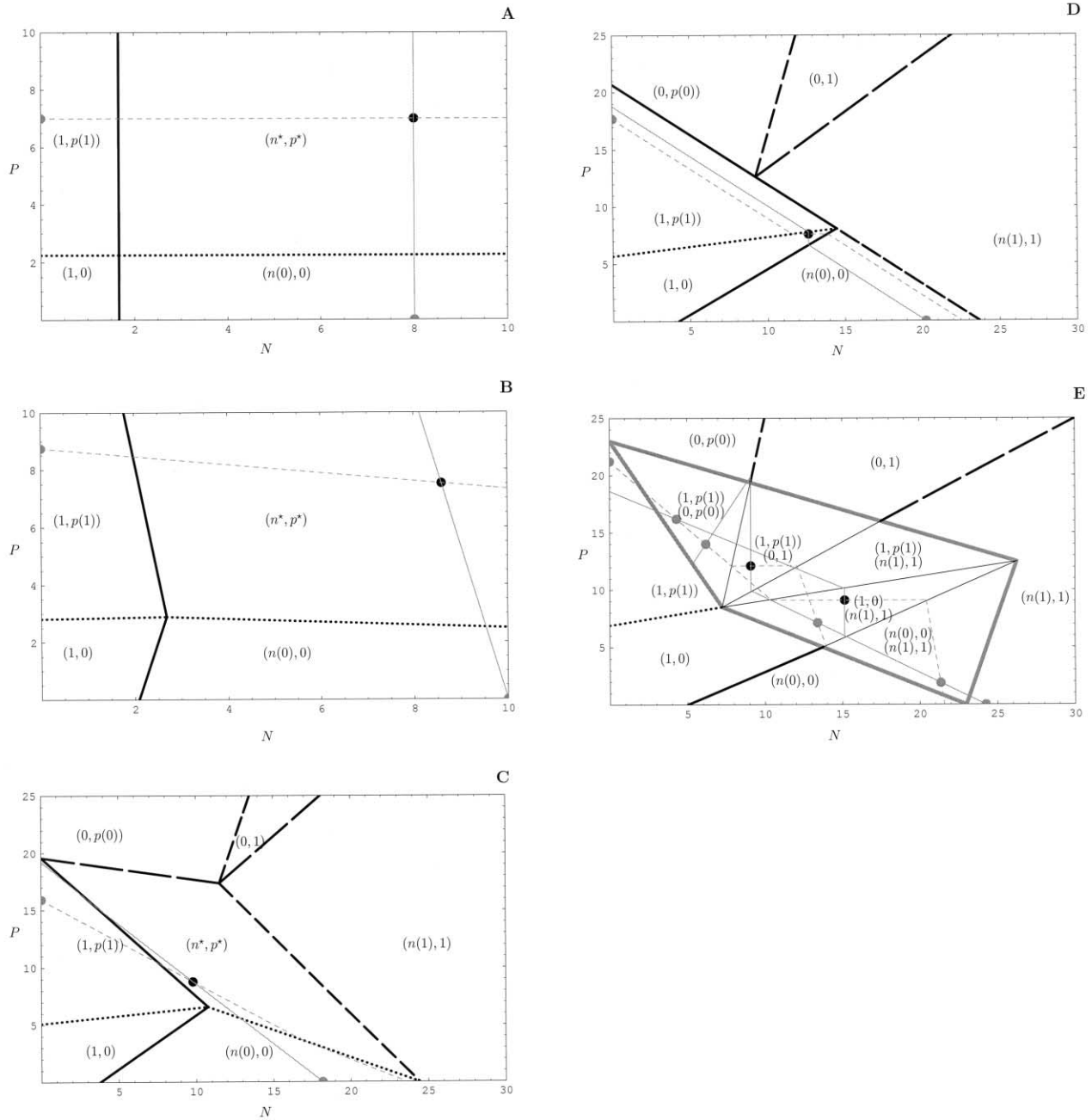
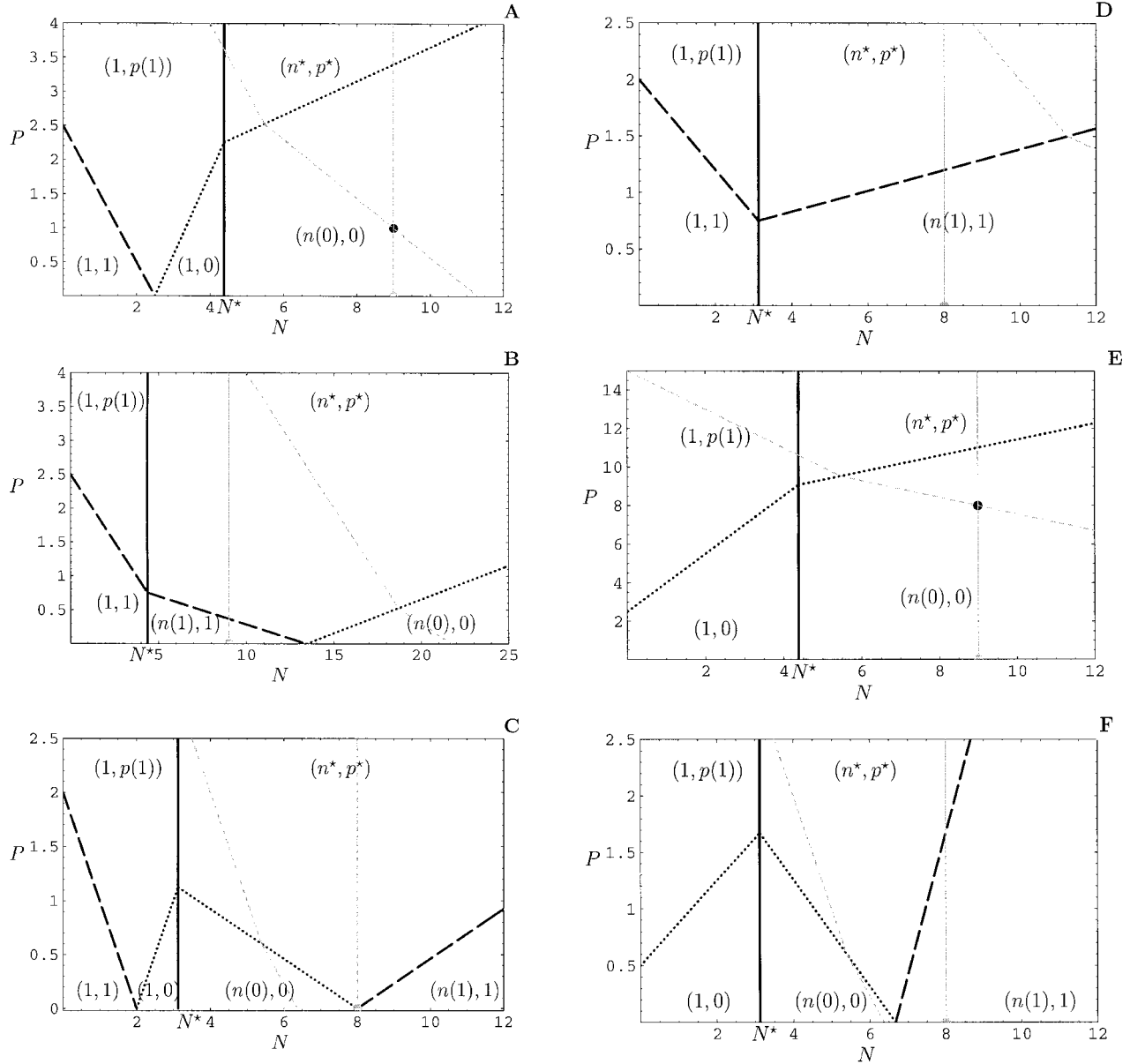


Figure 4: Habitat selection maps for the distinct-preference case ( $r_{p_1} = 1$ ,  $r_{p_2} = 4$ ); other parameters are the same as those given in figure 3

slowly with increasing interspecific density in habitat 1. That is why isoleg  $N_1^*$  shifts in a clockwise direction.

For higher levels of interspecific competition, isoleg  $N_1^*$  meets the  $P$ -axis, isoleg  $P_1^*$  meets the  $N$ -axis, and at these meeting points, 100% isolegs  $N_2^*$  and  $P_2^*$  appear.

These isolegs delimit regions of the density space in which populations  $N$  and  $P$ , respectively, specialize in the poorer habitat 2 (fig. 3C). To explain this rather surprising result, we discuss the effect of interspecific competition on the slopes of the isolegs. Consider, for example, figure 3C. We



**Figure 5:** Habitat selection map for the case in which species  $N$  is competitively dominant. This figure describes all qualitative possibilities for isoleg positions both for the shared-preference case (A–D) and the distinct-preference case (E, F). The vertical solid line is the isoleg for the dominant species. 0% isoleg ( $P_1^*$ ) is represented by the short dashed line and 100% isoleg ( $P_2^*$ ) by the dotted line. Proportions of species  $N$  and  $P$  in first habitat are given in parentheses. Gray lines are isoclines (solid line is the isocline for the first species; dashed line is the isocline for the second species). Locally stable equilibria are denoted by filled circles and those that are unstable by gray circles. Parameters in A:  $\alpha = 0, \beta = 1, K_{N_1} = 7, K_{N_2} = 2, K_{P_1} = 5, K_{P_2} = 3, r_{N_1} = 4, r_{N_2} = 1.5, r_{P_1} = 4, r_{P_2} = 2$ . Parameters in B:  $\alpha = 0, \beta = 0.4, K_{N_1} = 7, K_{N_2} = 2, K_{P_1} = 5, K_{P_2} = 3, r_{N_1} = 4, r_{N_2} = 1.5, r_{P_1} = 4, r_{P_2} = 2$ . Parameters in C:  $\alpha = 0, \beta = 1, K_{N_1} = 5, K_{N_2} = 3, K_{P_1} = 4, K_{P_2} = 2, r_{N_1} = 4, r_{N_2} = 1.5, r_{P_1} = 4, r_{P_2} = 2$ . Parameters in D:  $\alpha = 0, \beta = 0.4, K_{N_1} = 5, K_{N_2} = 3, K_{P_1} = 4, K_{P_2} = 2, r_{N_1} = 4, r_{N_2} = 1.5, r_{P_1} = 4, r_{P_2} = 2$ . Parameters in E:  $\alpha = 0, \beta = 1, K_{N_1} = 7, K_{N_2} = 2, K_{P_1} = 5, K_{P_2} = 10, r_{N_1} = 4, r_{N_2} = 1.5, r_{P_1} = 3, r_{P_2} = 4$ . Parameters in F:  $\alpha = 0, \beta = 1, K_{N_1} = 5, K_{N_2} = 3, K_{P_1} = 4, K_{P_2} = 2, r_{N_1} = 4, r_{N_2} = 1.5, r_{P_1} = 3, r_{P_2} = 4$ .

have explained why isoleg  $N_1^*$  for species  $N$  has a negative slope below isoleg  $P_1^*$ . In the case of increased interspecific competition relative to intraspecific competition (lower value of  $\sigma$ ; fig. 3C), habitat 1 becomes less suitable for species  $N$  at even lower densities of species  $P$ , making it more profitable for species  $N$  to specialize in the other habitat. Note that, depending on densities  $N$  and  $P$ , almost all distributions of the species are now possible. The only case that will never be observed is where both species occupy only the poor habitat. In figure 3C, we see that total spatial segregation between species  $N$  and  $P$  is possible. Depending on the density of both species, either species can occupy the poor habitat only. At high densities of both species, we observe the situation in which species  $N$  uses exclusively habitat 1 while species  $P$  does not use it at all (triangular area denoted by  $(1, 0)$ ). In this case, specializations at high densities can be understood by considering the qualitative values of the habitats because at high densities, species  $N$  is more affected by competition in habitat 2 than in habitat 1, while the opposite holds for species  $P$  (i.e.,  $r_{N_2}/K_{N_2} > r_{N_1}/K_{N_1}$  and  $r_{P_2}/K_{P_2} < r_{P_1}/K_{P_1}$ ). On the contrary, figure 3C also shows that distribution  $(0, 1)$  will be observed at low densities of species  $N$  and relatively low densities of species  $P$ . Although both species tend to prefer habitat 1 at low densities, the quantitative difference between habitats 1 and 2 is much stronger for species  $P$  than for species  $N$  ( $r_{P_1}/r_{P_2} = 4$ , while  $r_{N_1}/r_{N_2} = 1.5$ ). Thus, species  $P$  will tend to occupy only habitat 1, and because it is also the stronger interspecific competitor, it will outcompete species  $N$  and force it to move to habitat 2. Thus, as we have seen for the case of a single species, preferences at low species densities are influenced by quantitative differences between the habitats, while at high densities, they are influenced by qualitative differences between habitats. In addition to the single species case, in the case of two species, strength of interspecific competition must be also considered.

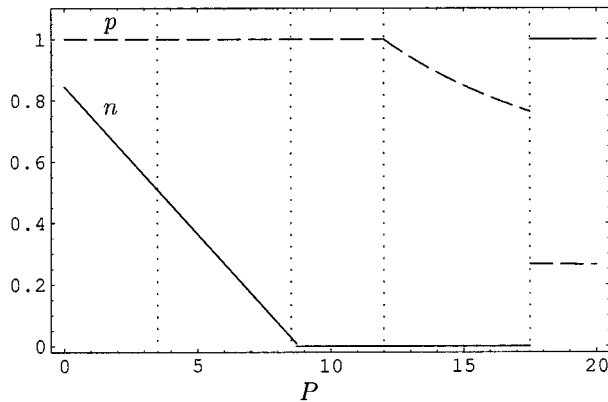
For relatively low interspecific competition (i.e., values of  $\sigma$  close to 1), the joint IFD is uniquely defined (fig. 3A–3C). As interspecific competition increases relative to intraspecific competition (i.e., as parameter  $\sigma$  decreases), the habitat selection map becomes increasingly complex because each species now has two isolegs (fig. 3C), but strategies still are uniquely defined for each set of species densities. There is a critical threshold for parameters at which 0% and 100% isolegs  $N_1^*$  and  $N_2^*$  and  $P_1^*$  and  $P_2^*$  partly coincide (fig. 3D). This happens when  $\alpha\beta = \alpha'\beta'(1 - \sigma)^2/\sigma^2 = 1$ , which gives

$$\sigma^* = \frac{1}{1 + 1/\sqrt{\alpha'\beta'}}.$$

If the strength of intraspecific competition relative to that of interspecific competition is equal to or below the critical value  $\sigma^*$ , then the region in which both species are generalist—i.e., the region marked by  $(n^*, p^*)$  in figure 3C—vanishes. Interspecific competition becomes so important compared to intraspecific competition that in all cases at least one species is excluded from one habitat. This situation arises because 0% and 100% isolegs cross in species-density space (fig. 3D). Thus, as species densities change, there may be sudden switches in species distributions from one habitat to the other. For example, increase in density of species  $N$ , for high enough densities of species  $P$ , can lead to a sudden switch of species  $N$  from habitat 2 to habitat 1 (transition from distribution  $(0, p(0))$  to distribution  $(1, p(1))$  in fig. 3D). Such discontinuous 0–1 transitions do not arise in situations with lower levels of interspecific competition (see fig. 3A–3C). In fact, nonuniqueness in species distributions does not allow us to define species isolegs in the part of the species-density space in which two possible IFDs exist (the region of species-density space bounded by the solid gray quadrangle in fig. 3D). The isolegs are well defined only outside of this quadrangle.

Because of 0% and 100% isoleg crossing, the resulting habitat selection map is no longer uniquely defined. This is because the region of density space in which, say, species  $N$  occupies habitat 1 only and the region where it occupies habitat 2 only partly overlap. The result is an apparently complex habitat selection map, with two possible IFDs always in the region of overlap (fig. 3E). Habitat selection outside this region can be interpreted by considering both the level of interspecific competition and the qualitative and quantitative differences between the habitats, for both species, as we discussed in the case of figure 3C.

The fact that isolegs and IFD are not uniquely defined for high interspecific competition does not preclude unique definition of IFD along population trajectories in species-density space, provided that the initial species distribution is given. For example, consider the transect in figure 3E, along which density of species  $N$  is constant and equal to 7.5 and density of species  $P$  increases from 0 to 20. Along this transect, IFD can be uniquely determined from figure 3E, and it is shown in figure 6. This is due to the “priority effect” that effectively selects one of the two possible species distributions when crossing boundaries of regions of the species-density space in which distributions qualitatively change. Along the transect species, distribution for low densities of species  $P$  is uniquely given by  $(n(1), 1)$ . This distribution will be kept when density of species  $P$  is such that the transect enters the region of species-density space in which IFD is not uniquely determined. Then distribution along the transect will switch to



**Figure 6:** IFD along a transect of  $E$  for constant density of species  $N = 7.5$ ; shows preference of  $N$  species (solid line) and of  $P$  species (dashed line) for habitat 1 as a function of increasing  $P$  species density. Along such transects IFD is uniquely defined if the initial population densities lie in the part of the species-density space where IFD is uniquely defined.

(0,  $p(0)$ ) and, finally, to (1,  $p(1)$ ). The last transition along the transect will be discontinuous.

#### The Distinct-Preference Case

Now we assume that the intrinsic per capita growth rate for species  $N$  is higher in habitat 1, while for species  $P$  it is higher in habitat 2 (i.e.,  $r_{N_1} > r_{N_2}$  and  $r_{P_1} < r_{P_2}$ ). Species  $N$  and  $P$  are sharing common resources but show different initial preferences. For example, one of them could be more efficient than the other at harvesting a particular type of resource (Morris et al. 2000). As a consequence, when densities are low, each species will inhabit only its preferred habitat (see fig. 4).

Again we study graphically the changes of the habitat selection map along the gradient given by the relative importance of interspecific competition represented by parameter  $\sigma$  (fig. 4). Isolegs show the same general tendencies: straight and perpendicular isolegs for the intraspecific case only become piecewise linear when interspecific competition is introduced in the model. Again, very high levels of interspecific competition lead to numerous possible distributions. When  $\alpha\beta > 1$  (which means that  $\sigma$  is below  $\sigma^*$ ), distribution of both species in both habitats becomes impossible, and isolegs are not uniquely defined in some regions of the species-density space (fig. 4E).

#### One Species Is Dominant

The ecological literature reports that interspecific competition is asymmetric in most situations (Schoener 1983).

Additionally, published habitat selection graphs demonstrate this situation for birds (Pimm et al. 1985) and rodents (Abramsky et al. 1990). That is why we now present a detailed study of the case wherein one species is dominant. We assume that species  $N$  is not affected by competition with species  $P$  in either habitat. As a consequence, competition coefficient  $\alpha = 0$ . Habitat selection by the dominant species  $N$  is not affected by the density of the subordinate species  $P$  and follows the rules given for a single population: it specializes in habitat 1 when at densities below the threshold  $N^*$  given by equation (1), and visits both habitats above that density, with a preference for habitat 1 given by equation (2). Because the dominant species never specializes in the poorer habitat, only the 0% isoleg exists for this species. This isoleg is a vertical line (fig. 5, heavy solid line).

By contrast, both 0% and 100% isolegs  $P_1^*$  (dashed heavy line) and  $P_2^*$  (dotted heavy line) exist for species  $P$ . Computation of IFD for this species follows from the general case and is given in appendix B. Here we briefly survey general properties of the subordinate species isolegs (see fig. 5 and app. B). We remark that because  $\alpha = 0$ , the condition  $\alpha\beta < 1$  is satisfied, and therefore, IFD is uniquely defined for all species densities and all parameter combinations. On the left side of the dominant species isoleg, that is, for low-dominant species density ( $N < N^*$ ), this species will occupy only the more profitable habitat 1. In the corresponding part of the population density space, the 0% isoleg for the subordinate species (dashed line, fig. 5) always has a negative slope and the 100% isoleg (dotted line, fig. 5) has a positive slope. This is because increasing the density of the dominant species in habitat 1 tends to lower the density above which animals of species  $P$  begin to colonize habitat 2 and to increase the density below which it pays for them to occupy habitat 2 only. Appendix B shows that the two subordinate species isolegs can intersect at most in two points that are on the  $N$ -axis. From the analysis given in appendix B, it follows that actual position of the subordinate species isolegs qualitatively depends on two critical relations among parameters. First, it depends on the value of competition coefficient  $\beta$  with respect to a threshold value of this coefficient given by

$$\beta^* = \frac{K_{P_1} r_{N_1} (r_{P_1} - r_{P_2})}{K_{N_1} r_{P_1} (r_{N_1} - r_{N_2})}.$$

We remark that for the shared-preference case ( $r_{P_1} > r_{P_2}$ ),  $\beta^*$  is positive while for the distinct-preference case it is negative. To the left of the dominant species isoleg, the two subordinate species isolegs intersect only if competition is strong ( $\beta > \beta^*$ ) and habitat 1 is preferred by both species ( $r_{P_1} > r_{P_2}$ , shared-preference case; fig. 5A, 5C).

Second, to give conditions under which the subordinate

species isolegs intersect to the right of the dominant species isoleg, we need to consider, in addition to the value of the competition coefficient, the following inequality, which relates to the input matching rules for the two species if considered alone (see “Distribution of a Single Population” and app. B):

$$\left(\frac{K_{P_1}}{r_{P_1}}\right)\left(\frac{K_{P_2}}{r_{P_2}}\right) < \left(\frac{K_{N_1}}{r_{N_1}}\right)\left(\frac{K_{N_2}}{r_{N_2}}\right). \tag{8}$$

Inequality (8) implicates that if we consider the two species separately, species *N* at high densities would prefer habitat 1 more strongly than would species *P*. It is shown in appendix B that the two subordinate species isolegs intersect to the right of the dominant species isoleg either if  $\beta > \beta^*$  and the opposite inequality to relation (8) holds (fig. 5C, 5F) or if competition is weak ( $\beta < \beta^*$ ) and inequality (8) holds (fig. 5B).

*The Shared-Preference Case*

We first consider the “shared-preference” case (i.e.,  $r_{N_1} > r_{N_2}$  and  $r_{P_1} > r_{P_2}$ ), in which both species prefer habitat 1 at low densities (fig. 5A–5D). When colonization begins, resources present in habitat 1 are more appealing for both species. As density of the dominant species (*N*) increases, the relative suitability of each habitat is now determined by whether individual success is strongly influenced by competition. In figure 5A and 5B, habitat 1 becomes less suitable for species *P* (in the sense that inequality [8] holds), and species *P* reverses its preference at high densities of the dominant species. In figure 5C and 5D, habitat 1, which was more attractive at low densities, is also the more suitable habitat at high densities for species *P* (in the sense that inequality [8] is reversed). Species *P* regains its original preference at high densities. This is because in crowded environments, habitat suitability is no longer determined by resource potential standing crop but by the way habitat value is affected by increasing numbers of consumers (Holt 1985; Morris 1988). In figure 5A and 5C, the per capita effect of interspecific competition is high, in the sense that  $\beta > \beta^*$ . As a consequence, we observe that total segregation is possible. For certain sets of densities, the dominant species stays in the best habitat and forces the subordinate species to stay in the poor habitat. If  $\beta < \beta^*$ , interspecific competition is too weak to make total segregation possible (see fig. 5B, 5D).

*The Distinct-Preference Case*

For the distinct-preferences case, the qualitative positions of isolegs are given in figure 5E and 5F. Contrary to the

shared-preferences case, at low densities of the dominant species, the subordinate species never specializes in habitat 1 regardless of its density. At high densities of the dominant species, however, the subordinate species can specialize in the less preferred habitat 1 (fig. 5F). This happens if inequality (8) is reversed, which means that the subordinate species will specialize in habitat 1 because the value of this habitat is less affected at high densities of consumers.

**Consequences for Population Dynamics**

The primary aim of our model was to derive habitat selection rules for all possible densities of conspecific and heterospecific competitors. We now study population distributions only at population equilibrium. This will show whether IFDs should promote coexistence between species. The classical Lotka-Volterra competition model extended to a two-habitat system with species distributions given by *n*, 1 – *n*, and *p*, 1 – *p*, is described by the following system:

$$\begin{aligned} \frac{dN}{dt} &= r_{N_1}nN\left(1 - \frac{nN}{K_{N_1}} - \frac{\alpha pP}{K_{N_1}}\right) \\ &+ r_{N_2}(1-n)N\left(1 - \frac{(1-n)N}{K_{N_2}} - \frac{\alpha(1-p)P}{K_{N_2}}\right), \\ \frac{dP}{dt} &= r_{P_1}pP\left(1 - \frac{pP}{K_{P_1}} - \frac{\beta nN}{K_{P_1}}\right) \\ &+ r_{P_2}(1-p)P\left(1 - \frac{(1-p)P}{K_{P_2}} - \frac{\beta(1-n)N}{K_{P_2}}\right). \end{aligned} \tag{9}$$

For fixed population distributions (i.e., for nonadaptive consumers that do not follow IFD), the above system is the classical Lotka-Volterra competition model with isoclines that are straight lines in density-state space. Depending on the position of isoclines, the model either has one interior equilibrium or one population outcompetes the other species. If the interior equilibrium exists, then it is globally stable if  $\alpha\beta < 1$ .

If species spatial distribution follows IFD, as described in the previous sections of this article, then isoclines become piecewise straight lines (*gray lines*, figs. 3–5; isocline for the first species is shown as a solid line while the isocline for the second species is shown as a dashed line). This is because isolegs split the density space into several regions, in each of which population dynamics are described by a Lotka-Volterra competition system with specific parameters; therefore, the slope of isoclines changes when isoclines cross the isolegs.

Appendix C shows that coexistence within both habitats at population equilibrium is possible if and only if  $\alpha < K_{N_1}/K_{P_1}$ ,  $\alpha < K_{N_2}/K_{P_2}$ ,  $\beta < K_{P_1}/K_{N_1}$ , and  $\beta < K_{P_2}/K_{N_2}$ . We remark that conditions  $\alpha < K_{N_1}/K_{P_1}$  and  $\beta < K_{P_1}/K_{N_1}$  are the conditions that permit stable coexistence in habitat 1, if it is isolated from the rest of the environment, while conditions  $\alpha < K_{N_2}/K_{P_2}$  and  $\beta < K_{P_2}/K_{N_2}$  permit stable coexistence in habitat 2. Hence, parameter values that permit species coexistence over the whole environment are also those that would allow coexistence within each habitat, if it is considered in isolation.

Complete segregation between habitats 1 and 2 at population equilibrium occurs if  $\alpha > K_{N_1}/K_{P_1}$  and  $\beta > K_{P_2}/K_{N_2}$  or if  $\alpha > K_{N_2}/K_{P_2}$  and  $\beta > K_{P_1}/K_{N_1}$  (see app. C). Hence, the sets of parameters that make segregation possible across the habitats are those that lead to competitive exclusion in single-habitat environments.

Figures 3 and 4 show that for low values of interspecific competition, both species occupy both habitats at population equilibrium (figs. 3A–3C, 4A–4C). Exclusion occurs when the relative strength of interspecific competition compared with intraspecific competition increases. In figures 3D and 4D, population equilibrium coincides with total segregation: species *N* is found only in habitat 1 and species *P* occupies only habitat 2. When interspecific competition is even stronger (i.e., when  $\alpha\beta > 1$ ), isoclines become very complicated, and multiple equilibria exist (figs. 3E, 4E). We note in figures 3E and 4E that two stable equilibria exist that coincide with segregation between species *N* and *P*. One corresponds to IFD (1, 0) and the other to IFD (0, 1). This is because  $\alpha > K_{N_1}/K_{P_1}$ ,  $\beta > K_{P_2}/K_{N_2}$ ,  $\alpha > K_{N_2}/K_{P_2}$ , and  $\beta > K_{P_1}/K_{N_1}$ . In the situations described in figures 3E and 4E, as well as those described in figures 3D and 4D, intense competition between species *N* and *P* will preclude their coexistence at a population equilibrium. Thus, we will observe the “ghost of competition” (Rosenzweig 1991; Morris 1999).

### Discussion

In this article we study the influence of intraspecific and interspecific competition on habitat selection behavior in a two-habitat environment. Our models consider either one or two competing species in a habitat that is composed of two habitats of different quality; the habitat selection strategy for a particular species is the proportion of time that its members spend in either habitat. We assume that animals maximize their instantaneous per capita population rate of increase, and we derive the ideal free distribution across habitats. This allows us to determine the exact shape of isolegs, which are the lines in species-density space that separate regions with qualitatively different species distributions (Rosenzweig 1981). The IFD has been

demonstrated many times in foraging groups (Milinski 1988; Dreisig 1995). When breeding behavior is considered, increasing densities of both conspecifics and heterospecifics lead to decreasing reproductive success (Gustafsson 1987). Also, breeding populations settling in heterogeneous environments may achieve IFD (Pierotti 1982; Wahlström and Kjellander 1995).

When applied to a single population, IFD theory predicts that below a certain density, all individuals will occupy the best part of their environment. Above this threshold, they will also spend some time in the poorer part of their habitat. This phenomenon has been called the “buffer effect” (Brown 1969; Sutherland 1996). Our model predicts the threshold density above which generalization should begin and a hyperbolic and decreasing relationship between the total population density and individual preference for the most profitable habitat (fig. 1). In a field study on feeding hummingbirds by Pimm et al. (1985) and reanalyzed by Rosenzweig (1986), the response of the dominant species is unaffected by interspecific competition and exhibits these particular patterns in close agreement with figure 1 (see also Rosenzweig 1991; Rosenzweig and Abramsky 1997). Other studies are also in qualitative agreement with our prediction (Zwarts 1976; Goss-Custard 1977).

Several field studies focused on interactions between a dominant and a subordinate species with similar habitat preferences (Pimm et al. 1985; Abramsky et al. 1990; Bourke et al. 1999; Morris et al. 2000). In accordance with our predictions, they show that the dominant species will stay in the best parts of their environment at low density and will invade all parts when their density exceeds a certain threshold. Pimm et al. (1985), Abramsky et al. (1990), Suhling (1996), and Bourke et al. (1999) observed that increasing the density of either subordinate or dominant species may increase the use of the poorest parts of the environment by a subordinate species. These observations are compatible with our predictions. So is the observation that at very high densities of the dominant species, the subordinate species may be forced to inhabit only these poor areas (Pimm et al. 1985; Bowers et al. 1987; Franke and Janke 1998).

We predict that the 0% isoleg for the subordinate species always has a negative slope on the left side of the dominant species isoleg. Pimm et al. (1985) suggested that the subordinate isoleg may intersect the dominant species axis either to the left or to the right of the dominant species isoleg. Our model shows that both cases are possible, intersection to the left of the dominant species isoleg being conditioned by intense competitive effect of the dominant species on the subordinate species. Our analysis predicts that there are more qualitative cases because, depending on parameter values, either isoleg for the subordinate spe-

cies can intersect the dominant species isoleg (fig. 5). Moreover, isolegs are not straight lines; they are piecewise linear. Our model predicts that if the 0% isoleg for the subordinate species crosses the isoleg of the dominant species, then its orientation changes in a counterclockwise manner (fig. 5B, 5D). This happens because to the right of the dominant species isoleg, the dominant species also visits habitat 2, and so increasing its density does not solely affect the fitness of the subordinate species in habitat 1. If interspecific competition is strong enough, then both isolegs for the subordinate species will be observed on the left side of the dominant species isoleg (fig. 5A, 5C). In this case, the 100% isoleg for the subordinate species will cross the dominant species isoleg at a sharp angle, with declining slope to the right of the intersection. If inequality (8) does not hold, then the slope becomes negative and the 0% isoleg will reappear with a positive slope on the right side of the dominant species isoleg (fig. 5C). In that situation, the subordinate species switches its habitat preference twice as the density of the dominant species increases. The reason for this particular behavior is that the ratio of habitat qualitative values is higher for the subordinate species than for the dominant (i.e., inequality [8] does not hold). Thus, preference of the subordinate species for habitat 1 is more marked at high densities than preference of the dominant species for this habitat, and it will specialize in habitat 1 at high densities, just as it did at low densities but for a different reason.

In a recent study, Morris et al. (2000) traced the habitat selection map for asymmetric competition between two species of lemmings with distinct preferences. This map is qualitatively similar to our figure 5F and shows the strong discontinuity in the direction of the isoleg of the 100% species when it crosses that of the dominant. Morris et al. (2000) did not observe the second isoleg for the subordinate species. Their study does not, however, preclude the existence of this isoleg.

In conclusion, for the case of asymmetric competition, our model predicts that both isolegs for the subordinate species should meet at a sharp angle when crossing the dominant species isoleg, that the 0% isoleg may consist of two separated lines, and that the 100% isoleg may not exist at all. It also predicts that whenever any of the two isolegs of a subordinate species intersects the dominant species axis, then the other isoleg will also cross that particular intersection point too.

Although ecological reviews stress that asymmetric competition is very common in nature, our study proposes a general method to derive IFD for habitat selection even in cases of more balanced interspecific competition. Derivation of IFD for this case is more complicated because distribution of species 1 depends on distribution of species 2 and vice versa. The solution to this problem that assures

that neither species can increase its fitness by changing its strategy requires a game theoretical approach (Maynard Smith 1982; Thomas 1986; Hofbauer and Sigmund 1998). Our model predicts that as the strength of interspecific competition increases, complexity of habitat selection maps increases too. When interspecific competition is very strong when compared to intraspecific competition, 0% and 100% isolegs for one species can cross, which leads to nonuniqueness in species distributions in some regions of the density space. In these situations, the model predicts that habitat selection will lead to habitat segregation between species at the population equilibrium, thus creating the “ghost of competition” (Rosenzweig 1991; Morris 1999; see fig. 3D, 3E; fig. 4D, 4E).

The prediction that the isolegs for each species should change direction when crossing those of the other species is ubiquitous in our model. It emerges as soon as we consider even low levels of interspecific competition, and we believe it to be of general value. As stated above, such deflections have already been mapped for natural systems (Morris et al. 2000). In contrast, the particular prediction that more than one IFD may be possible for certain sets of densities only applies to situations with extremely high levels of interspecific competition. We remark that the condition required for the existence of multiple IFDs (i.e.,  $\alpha\beta > 1$ ) also precludes stable coexistence between the two species in both habitats. Thus, multiple IFDs are possible only for extreme levels of interspecific competition, and even then will not be observed if the system is close to a population equilibrium. In other words, multiple IFDs are expected only during the transitory phase that will finally lead two highly competitive species to total segregation. Although it is doubtless important to explore global possibilities, the consideration above certainly limits the likelihood of occurrence of the most complex of the habitat selection maps (namely, fig. 3E for the case of shared preferences and fig. 4E for the case of distinct preferences, where high levels of interspecific competition are even less expected).

Our predictions were obtained from a Lotka-Volterra model, which yields linear fitness functions similar to some functions already used in habitat selection theory (Pimm and Rosenzweig 1981; Morris 1987, 1994, 1999). These functions permit us to represent both qualitative and quantitative richness of habitats, which in reality may vary in different ways for competing species (Ovadia and Abramsky 1995). Morris et al. (2000) state that real fitness functions should be curvilinear (see also Morris 1989; Wilson and Yoshimura 1994), although linear fitness density lines have been reported too (Ovadia and Abramsky 1995). One characteristic of these fitness functions is that they assume full competition between species as soon as they begin to use the same habitat. However, even linear fitness

functions can predict complex behavioral patterns, sometimes with more than one possible outcome. Also, piecewise linear isolegs may be relevant approximations of real isolegs, which most likely are not linear (Pimm and Rosenzweig 1981).

The assumption that competition coefficients are the same in both habitats is also simplifying, since the level of exploitative competition may depend on the resources present in the habitat as well as the level of aggressiveness between species (Hairston 1980). The model could be made more realistic by including different competition coefficients in habitats 1 and 2, as has already been done with other kinds of models (isodars; Morris (1988)).

There exists a large literature that aims to understand how resource or habitat partitioning may allow coexistence between competing species (Schoener 1974*a*, 1974*b*, 1974*c*; Connell 1980). Moreover, both theoretical and experimental explorations strongly suggest that habitat selection strategies play a role in the initiation of sympatric speciation by favoring isolation between species (Rice and Salt 1988; Johannesson 2001). Our model shows that adaptive rules for habitat selection may indeed lead to segregation of competing species across different parts of the environment. However, the model also shows that high levels

of competition are necessary for segregation across the habitats at population equilibrium. This prediction agrees with observations that high levels of interference tend to reduce overlap between distribution areas of neighboring and competing species, making borderlines (Brown 1971; Hairston 1980). Hence, adaptive strategies for habitat choice in heterogeneous environments may lead to segregation between species. This may allow coexistence at the scale of the whole environment, if we observe reciprocal exclusion as well as favor the initial steps of sympatric speciation by allowing reproductive isolation. However, our models suggest that this will be possible only if high levels of competition between species already exist.

#### Acknowledgments

We thank D. Moorhead and D. Morris for their useful suggestions. This research was partially supported by the Grant Agency of the Czech Republic (201/98/0227), by the Institute of Entomology (Academy of Sciences of the Czech Republic Z5007907, K6005114), and by the Ministry of Education, Youth, and Sports (MŠM 123100004).

### APPENDIX A

#### Habitat Selection Map: The General Case

In this appendix we compute ideal free distribution (IFD) for two competing species in a two-habitat environment. First we compute all distributions of both species such that no individual can increase its fitness by playing a different strategy. In game theory these strategies are called noncooperative Nash equilibria (Thomas 1986). Then we select those that are stable with respect to small spatial perturbations. These latter are those that we call IFDs.

In order to compute Nash equilibria we follow the standard approach (Thomas 1986). First we compute the best distribution of species  $N$  for any fixed distribution of species  $P$  and conversely. The intersections of these two functions define the Nash equilibrium points. The IFD strategy  $n$  of species  $N$  for every distribution  $p$  of species  $P$  is

$$n(p) = \begin{cases} 1 & \text{if } p < p_1 \\ \frac{K_{N_1}[K_{N_2}(r_{N_1} - r_{N_2}) + r_{N_2}(N + \alpha P)]}{N(K_{N_2}r_{N_1} + K_{N_1}r_{N_2})} - \frac{p\alpha P}{N} & \text{if } p_1 \leq p \leq p_2 \\ 0 & \text{if } p > p_2, \end{cases}$$

where

$$p_1 = \frac{K_{N_1}K_{N_2}(r_{N_1} - r_{N_2}) + \alpha K_{N_1}r_{N_2}P - K_{N_2}r_{N_1}N}{\alpha P(K_{N_2}r_{N_1} + K_{N_1}r_{N_2})},$$

$$p_2 = \frac{K_{N_1}[K_{N_2}(r_{N_1} - r_{N_2}) + r_{N_2}(N + \alpha P)]}{\alpha P(K_{N_2}r_{N_1} + K_{N_1}r_{N_2})}. \quad (\text{A1})$$

Similarly, for a fixed strategy  $n$  of species  $N$ , the IFD strategy  $p$  of species  $P$  satisfies



$$p(n) = \begin{cases} 1 & \text{if } n < n_1 \\ \frac{K_{p_1}[K_{p_2}(r_{p_1} - r_{p_2}) + r_{p_2}(\beta N + P)]}{P(K_{p_2}r_{p_1} + K_{p_1}r_{p_2})} - \frac{n\beta N}{P} & \text{if } n_1 \leq n \leq n_2 \\ 0 & \text{if } n_2 \leq n, \end{cases}$$

where

$$\begin{aligned} n_1 &= \frac{K_{p_1}K_{p_2}(r_{p_1} - r_{p_2}) + \beta K_{p_1}r_{p_2}N - K_{p_2}r_{p_1}P}{\beta N(K_{p_2}r_{p_1} + K_{p_1}r_{p_2})}, \\ n_2 &= \frac{K_{p_1}[K_{p_2}(r_{p_1} - r_{p_2}) + r_{p_2}(P + \beta N)]}{\beta N(K_{p_2}r_{p_1} + K_{p_1}r_{p_2})}. \end{aligned} \tag{A2}$$

The points where the two piecewise linear lines  $n(p)$  and  $p(n)$  cross-define distributions of both species such that no individual can increase its fitness by playing a different strategy. However, not all of them are stable with regard to small perturbations in strategies. Those that are stable (shown as filled circles in fig. 2) are characterized by the property that the slope of the inverse function of  $n(p)$ , which is  $-N/(\alpha P)$ , is smaller than is the slope of  $p(n)$ , which is  $-\beta N/P$  (see fig. 2*h*). Here we give a complete classification of IFD. The structure of the IFD set depends on the position of  $p_1$ ,  $n_1$ ,  $p_2$ ,  $n_2$ ,  $p(0)$ ,  $p(1)$ ,  $n(0)$ , and  $n(1)$ . Because of our assumption that  $r_{N_1} > r_{N_2}$ ,  $p_2$  is always positive. Moreover,  $p_1 < p_2$  and  $n_1 < n_2$ . Because the curves  $n(p)$  and  $p(n)$  are piecewise linear and constrained by values 0 and 1, they can intersect at most at three points (fig. 2), if we do not consider those parameter values for which the two curves coincide. The interior intersection point that corresponds to the case in which both species occupy both habitats is denoted by  $(n^*, p^*)$ , where

$$n^* = \frac{K_{N_1}[K_{N_2}(r_{N_1} - r_{N_2}) + r_{N_2}(N + \alpha P)]}{N(K_{N_2}r_{N_1} + K_{N_1}r_{N_2})} - \frac{p^*\alpha P}{N}$$

and

$$p^* = \frac{K_{p_1}[K_{p_2}(r_{p_1} - r_{p_2}) + r_{p_2}(P + N\beta)]}{P(1 - \alpha\beta)(K_{p_2}r_{p_1} + K_{p_1}r_{p_2})} - \frac{K_{N_1}[K_{N_2}(r_{N_1} - r_{N_2}) + r_{N_2}(N + P\alpha)]\beta}{P(1 - \alpha\beta)(K_{N_2}r_{N_1} + K_{N_1}r_{N_2})}.$$

Here we categorize possible IFD with respect to their position in the unit square  $(0, 1) \times (0, 1)$  (fig. 2).

(a) If  $n(1) = 1$  and  $p(1) = 1$ , then IFD is  $(1, 1)$ .

Otherwise we have

- (b) If  $n(0) < n_2$ ,  $n(1) < n_1$ ,  $p(0) < p_2$ , and  $p(1) > p_1$ , then IFD is  $(n(1), 1)$ .
- (c) If  $n(0) < n_2$ ,  $n(1) < n_1$ ,  $p(0) > p_2$ , and  $p(1) > p_1$ , then IFD is  $(0, 1)$ .
- (d) If  $n(0) < n_2$ ,  $n(1) > n_1$ ,  $p(0) > p_2$ , and  $p(1) > p_1$ , then IFD is  $(0, p(0))$ .
- (e) If  $n(0) < n_2$ ,  $n(1) > n_1$ ,  $p(0) < p_2$ , and  $p(1) < p_1$ , then IFD is  $(1, p(1))$ .
- (f) If  $n(0) > n_2$ ,  $n(1) > n_1$ ,  $p(0) < p_2$ , and  $p(1) < p_1$ , then IFD is  $(1, 0)$ .
- (g) If  $n(0) > n_2$ ,  $n(1) > n_1$ ,  $p(0) < p_2$ , and  $p(1) > p_1$ , then IFD is  $(n(0), 0)$ .
- (h) If  $n(0) < n_2$ ,  $n(1) > n_1$ ,  $p(0) < p_2$ , and  $p(1) > p_1$ , then IFD is  $(n^*, p^*)$ .
- (i) If  $n(0) < n_2$ ,  $n(1) < n_1$ ,  $p(0) < p_2$ , and  $p(1) < p_1$ , then IFD are  $(1, p(1))$  and  $(n(1), 1)$ .
- (j) If  $n(0) > n_2$ ,  $n(1) < n_1$ ,  $p(0) < p_2$ , and  $p(1) < p_1$ , then IFD are  $(1, 0)$  and  $(n(1), 1)$ .
- (k) If  $n(0) > n_2$ ,  $n(1) < n_1$ ,  $p(0) < p_2$ , and  $p(1) > p_1$ , then IFD are  $(n(0), 0)$  and  $(n(1), 1)$ .
- (l) If  $n(0) > n_2$ ,  $n(1) < n_1$ ,  $p(0) > p_2$ , and  $p(1) > p_1$ , then IFD are  $(n(0), 0)$  and  $(0, 1)$ .
- (m) If  $n(0) > n_2$ ,  $n(1) > n_1$ ,  $p(0) > p_2$ , and  $p(1) > p_1$ , then IFD are  $(n(0), 0)$  and  $(0, p(0))$ .
- (n) If  $n(0) > n_2$ ,  $n(1) < n_1$ ,  $p(0) > p_2$ , and  $p(1) < p_1$ , then IFD are  $(1, 0)$  and  $(0, 1)$ .
- (o) If  $n(0) < n_2$ ,  $n(1) > n_1$ ,  $p(0) > p_2$ , and  $p(1) < p_1$ , then IFD are  $(1, p(1))$  and  $(0, p(0))$ .

- (p) If  $n(0) > n_2$ ,  $n(1) > n_1$ ,  $p(0) > p_2$ , and  $p(1) < p_1$ , then IFD are (1, 0) and (0,  $p(0)$ ).
- (q) If  $n(0) < n_2$ ,  $n(1) < n_1$ ,  $p(0) > p_2$ , and  $p(1) < p_1$ , then IFD are (0, 1) and (1,  $p(1)$ ).

## APPENDIX B

### Isolegs Analysis for the Dominant Case

Here we analyze the isoleg position for the case in which species  $N$  is dominant. Because the dominant species  $N$  is not affected by competition with species  $P$  (competition coefficient  $\alpha = 0$ ) in either habitat, it distributes as if it were alone. First we assume that the density for the dominant species is below  $N^*$  (see formula [1]); that is, it occupies only habitat 1 ( $n^* = 1$ ). Then IFD of the subordinate species  $P$  is

$$p^* = \begin{cases} 1 & \text{if } P < P_1^* \\ \frac{K_{P_1}K_{P_2}(r_{P_1} - r_{P_2}) - \beta K_{P_2}r_{P_1}N + K_{P_1}r_{P_2}P}{P(K_{P_2}r_{P_1} + K_{P_1}r_{P_2})} & \text{if } P \geq \max(P_1^*, P_2^*) \\ 0 & \text{if } P < P_2^*, \end{cases}$$

where

$$P_1^* = \frac{K_{P_1}K_{P_2}(r_{P_1} - r_{P_2}) - \beta K_{P_2}r_{P_1}N}{K_{P_2}r_{P_1}}$$

$$P_2^* = \frac{-K_{P_1}K_{P_2}(r_{P_1} - r_{P_2}) + \beta K_{P_2}r_{P_1}N}{K_{P_1}r_{P_2}}. \quad (\text{B1})$$

Functions of the dominant species density  $P_1^*$  and  $P_2^*$  are 0% and 100% isolegs, respectively. The two isolegs intersect on the  $N$ -axis at the point

$$\frac{K_{P_1}(r_{P_1} - r_{P_2})}{\beta r_{P_1}}.$$

The intersection point is to the left of the point  $N^*$  if  $\beta > \beta^*$ . If  $N > N^*$ , then the dominant species occupies both habitats (see eq. [2]), and the distribution of the subordinate species is given by

$$p^* = \begin{cases} 1 & \text{if } P < P_1^* \\ \frac{\beta K_{N_1}K_{N_2}(r_{N_2} - r_{N_1})}{(K_{N_2}r_{N_1} + K_{N_1}r_{N_2})P} + \frac{\beta(K_{N_2}K_{P_1}r_{N_1}r_{P_2} - K_{N_1}K_{P_2}r_{N_2}r_{P_1})N}{(K_{N_2}r_{N_1} + K_{N_1}r_{N_2})(K_{P_2}r_{P_1} + K_{P_1}r_{P_2})P} \\ \quad + \frac{K_{P_1}[K_{P_2}(r_{P_1} - r_{P_2}) + r_{P_2}P]}{(K_{P_2}r_{P_1} + K_{P_1}r_{P_2})P} & \text{if } P \geq \max(P_1^*, P_2^*) \\ 0 & \text{if } P < P_2^*, \end{cases}$$

where

$$P_1^* = \frac{K_{P_1}(r_{P_1} - r_{P_2})}{r_{P_1}} + \frac{-\beta K_{N_1}K_{N_2}(r_{N_1} - r_{N_2})(K_{P_2}r_{P_1} + K_{P_1}r_{P_2}) + \beta(-K_{N_1}K_{P_2}r_{N_2}r_{P_1} + K_{N_2}K_{P_1}r_{N_1}r_{P_2})N}{K_{P_2}(K_{N_2}r_{N_1} + K_{N_1}r_{N_2})r_{P_1}},$$

$$P_2^* = \frac{-K_{P_2}(r_{P_1} - r_{P_2})}{r_{P_2}} + \frac{\beta K_{N_1}K_{N_2}(r_{N_1} - r_{N_2})(K_{P_2}r_{P_1} + K_{P_1}r_{P_2}) + \beta(K_{N_1}K_{P_2}r_{N_2}r_{P_1} - K_{N_2}K_{P_1}r_{N_1}r_{P_2})N}{K_{P_1}(K_{N_2}r_{N_1} + K_{N_1}r_{N_2})r_{P_2}}. \quad (\text{B2})$$

The two isolegs  $P_1^*$  and  $P_2^*$  intersect on the  $N$ -axis at the point

$$\frac{K_{P_1}K_{P_2}(K_{N_2}r_{N_1} + K_{N_1}r_{N_2})(r_{P_1} - r_{P_2}) - \beta K_{N_1}K_{N_2}(r_{N_1} - r_{N_2})(K_{P_2}r_{P_1} + K_{P_1}r_{P_2})}{\beta(K_{N_1}K_{P_2}r_{N_2}r_{P_1} - K_{N_2}K_{P_1}r_{N_1}r_{P_2})}.$$

This intersection point is to the right of  $N^*$  if either inequality (8) holds and  $\beta < \beta^*$  or the opposite inequality to inequality (8) holds and  $\beta > \beta^*$ .

## APPENDIX C

### Coexistence

#### *Analysis of the Interior Equilibrium*

Here we determine the conditions under which coexistence in both habitats is stable from both evolutionary and population dynamics points of view. In the region of the density space where IFD is given by  $(n^*, p^*)$ , population dynamics are given by

$$\begin{aligned} \frac{dN}{dt} &= \frac{r_{N_1}r_{N_2}N(K_{N_1} + K_{N_2} - N - P\alpha)}{K_{N_2}r_{N_1} + K_{N_1}r_{N_2}}, \\ \frac{dP}{dt} &= \frac{r_{P_1}r_{P_2}P(K_{P_1} + K_{P_2} - P - N\beta)}{K_{P_2}r_{P_1} + K_{P_1}r_{P_2}}. \end{aligned} \quad (C1)$$

Densities at population equilibrium are given by  $N_{\text{eq}} = [K_{N_1} + K_{N_2} - \alpha(K_{P_1} + K_{P_2})]/(1 - \alpha\beta)$  and  $P_{\text{eq}} = [K_{P_1} + K_{P_2} - \beta(K_{N_1} + K_{N_2})]/(1 - \alpha\beta)$ . Equilibrium  $(N_{\text{eq}}, P_{\text{eq}})$  exists and is stable for population dynamics if  $\alpha < (K_{N_1} + K_{N_2})/(K_{P_1} + K_{P_2})$  and  $\beta < (K_{P_1} + K_{P_2})/(K_{N_1} + K_{N_2})$ , which also implies that  $\alpha\beta < 1$ . Moreover, the equilibrium  $(N_{\text{eq}}, P_{\text{eq}})$  lies in the part of the state space where IFD is given by  $(n^*, p^*)$  provided inequalities *h* of appendix A are satisfied.

These inequalities evaluated in  $(N_{\text{eq}}, P_{\text{eq}})$  are  $\alpha < K_{N_1}/K_{P_1}$ ,  $\alpha < K_{N_2}/K_{P_2}$ ,  $\beta < K_{P_1}/K_{N_1}$ , and  $\beta < K_{P_2}/K_{N_2}$ . From these four inequalities,  $\alpha < (K_{N_1} + K_{N_2})/(K_{P_1} + K_{P_2})$ ,  $\beta < (K_{P_1} + K_{P_2})/(K_{N_1} + K_{N_2})$ , and  $\alpha\beta < 1$ , which implies that equilibrium  $(N_{\text{eq}}, P_{\text{eq}})$  exists and is stable from the population dynamics point of view.

#### *Segregation*

Here we seek the conditions under which, at population equilibrium, species  $N$  will inhabit only habitat 1 while species  $P$  will specialize in habitat 2. The corresponding IFD will be  $(1, 0)$ , and in the corresponding region of the density space, population dynamics are given by

$$\begin{aligned} \frac{dN}{dt} &= r_{N_1}N\left(1 - \frac{N}{K_{N_1}}\right), \\ \frac{dP}{dt} &= r_{P_2}P\left(1 - \frac{P}{K_{P_2}}\right). \end{aligned} \quad (C2)$$

The densities at equilibrium will be  $N_{\text{eq}} = K_{N_1}$  and  $P_{\text{eq}} = K_{P_2}$ . This equilibrium is stable from the population dynamics point of view. Equilibrium  $(N_{\text{eq}}, P_{\text{eq}})$  is in the part of the state space where IFD is given by  $(1, 0)$  in one of the following cases: *f*, *j*, *n*, and *p* of appendix A and figure 2. The conditions that hold in the corresponding region of the density space are  $n_2 < 1$  and  $p_1 > 0$ . These inequalities evaluated in  $(N_{\text{eq}}, P_{\text{eq}})$  are  $\beta > K_{P_1}/K_{N_1}$  and  $\alpha > K_{N_2}/K_{P_2}$ . Finally, these two inequalities are necessary and sufficient for complete species segregation at equilibrium, with species  $N$  specializing in habitat 1 and species  $P$  specializing in habitat 2. In a similar way, we can show that if  $\beta > K_{P_2}/K_{N_2}$  and  $\alpha > K_{N_1}/K_{P_1}$ , total segregation is again possible, but this time species  $N$  specializes in habitat 2 and species  $P$  in habitat 1.

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