

Has the ghost of competition passed?

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ABSTRACT

Theories of density-dependent habitat selection suggest that habitat-selecting competitors may stably co-exist in separate habitats with no competition (the ghost of competition past). The habitat distribution, and hence the value of the non-linear competition coefficients, depends on the joint densities of the competing species. I extend the theories to illustrate how non-linear effects arise from constant habitat-dependent competition. The habitat effect is easily estimated from census data by the use of habitat isodars (lines along which expected fitness is identical in both habitats). The isodar solutions not only reveal the ghost of competition, they can be used as a convenient assay for conditions of stable competitive co-existence and they allow calculation of the actual competition coefficients. The shapes of empirical isoclines are in general agreement with the theoretical predictions.

Keywords: co-existence, competition, ghost of competition, habitat selection, isocline, isodar, isoleg.

INTRODUCTION

Habitat selection is such a pervasive and efficient mechanism to resolve competition that competing species may often reside, at equilibrium, in different habitats (Rosenzweig, 1974, 1979, 1981, 1991; Pimm *et al.*, 1985). The competitive isoclines, whose slope and inverse slope represent the respective competition coefficients, are warped by habitat selection to intersect at right angles (no competitive effect; Rosenzweig, 1979, 1981; Pimm and Rosenzweig, 1981). Competitively mediated habitat selection thus creates the disturbing paradox that the competition responsible for habitat segregation lurks as the ‘ghost of competition past’ (Rosenzweig, 1979, 1981, 1991), which is invisible at the point of equilibrium.

How is one to measure competition in such a system and how is one to evaluate the stability of competitive co-existence if one cannot measure competition near the equilibrium? The answers must evaluate how habitat selection by individuals is influenced by conspecific and interspecific densities. I begin by briefly reviewing two approaches that offer promise of a solution, then develop the theory that illustrates how census data can be used both to estimate competition and to reveal competitive ghosts.

HABITAT-DEPENDENT ESTIMATES OF INTERSPECIFIC COMPETITION

When competing species co-exist in a habitat, they should depress the population densities of their competitors below the levels that they would otherwise attain. We should, therefore, be able to estimate the competitive effects of interacting species from the regression coefficients of their joint densities if we control for the effects of density-dependent habitat selection (Schoener, 1974, 1985; Crowell and Pimm, 1976; Hallett and Pimm, 1979; Pimm, 1985; Morris, 1988, 1989; Fox and Luo, 1996; but see Rosenzweig *et al.*, 1985; Abramsky *et al.*, 1986).

One solution, based on ideal habitat selection, relies on the analysis of habitat isodars, lines of density along which the expected fitness of individuals is equivalent in pairs of habitats (Morris, 1988). Isodars explicitly control for density-dependent habitat effects because they represent the solution, in density space, of evolutionarily stable habitat selection strategies. Interspecific density-dependent effects in each habitat can be included by multiple regression (e.g. Morris, 1989; Rodríguez, 1995); the partial regression coefficients represent the competition coefficients for each habitat. Isodar analysis allows the habitat selectors to define habitat (e.g. Knight and Morris, 1996) and thereby reduces investigator bias in the assessment of competition. But isodars have been criticized because they assume that competition coefficients are constant within habitats (Ovadia and Abramsky, 1995) when experiments on two species of co-existing gerbils reveal that interspecific competition varies with density (Abramsky *et al.*, 1991).

The gerbil experiments represent a clever alternative based on isoleg theory, another extension of ideal habitat selection. Isolegs are boundaries in density space that separate regions of equal habitat choice (Rosenzweig, 1979, 1981, 1991). A target species is established in two identical and adjacent plots and allowed to equalize its use of both. A known number of interspecific competitors is added to one of the plots. The change in habitat distribution of the target species represents the density-dependent effect of the competitor (Abramsky *et al.*, 1991, 1992, 1994). Replication of the experiment across a range of densities allows one to draw the entire isocline. The dramatic non-linear isoclines produced by the experiment confirm habitat selection's role in creating the ghost of competition (Abramsky *et al.*, 1991, 1992, 1994).

Isodars and isoclines estimate different competition coefficients. The isodar coefficient represents the average habitat-dependent effect of heterospecific individuals. The isocline coefficient is the average effect of all heterospecific individuals regardless of which habitat they or their competitor occupies. We should not expect them to be equivalent. But there should, nevertheless, be relatively simple transformations from one to the other, because both are based on common theories of density-dependent habitat selection.

I illustrate the transformations by deriving both isodar and isoleg theories from their underlying fitness-density curves. Each isoleg corresponds to a single point along its respective isodar. I review how isolegs warp isoclines and show that constant density-dependent competition coefficients obtained from isodars warp isoclines in exactly the same way to generate ghosts of competition. I illustrate how one can use isodars to estimate the variable slope of non-linear isoclines (the ghost of competition) and to examine the influences of spatial scale. I then contrast the predictions with Abramsky and Rosenzweig's gerbil isoclines (Abramsky *et al.*, 1991, 1992, 1994). I conclude with a short discussion on the relative uses of constant versus variable competition coefficients and how they relate to the ghost of competition past.

ISODARS AND ISOLEGS

Imagine, first, a species that can use two habitats that vary in their ability to contribute to fitness at different densities (Fig. 1). Individuals should preferentially occupy the habitat that yields the greatest contribution to fitness (Fretwell and Lucas, 1970). At low density, all individuals occupy the better habitat (habitat A in the example), but as fitness declines with increased density, individuals should, at some threshold density, begin to occupy the second habitat. The question we wish to answer is: ‘What is the average per capita effect of competing individuals on habitat choice?’ We can easily solve the problem by comparing the density of individuals in the preferred habitat (A) with the density of individuals occupying the less preferred habitat (B) (Fig. 1b). If one assumes that individuals use habitats in a way that maximizes fitness, the regression represents an isodar along which the expectation of fitness is equivalent in both habitats (Morris, 1988).

Assuming linear fitness functions, the isodar for species 1 is given by:

$$N_{1A} = C + bN_{1B} \tag{1}$$

where N equals population density, C is the maximum density of individuals occupying habitat A when the density in habitat B is zero, and the slope, b , is the ratio of the slopes of the underlying fitness-density curves (Morris, 1988). The isodar is the solution to an evolutionarily stable strategy of ideal density-dependent habitat selection (Morris, 1996a). A slope greater than 1 implies, for example, that the effect of a single individual on fitness is greater in habitat B than it is in habitat A. The essential point is that the slope of the isodar measures the relative effects on fitness of competing intraspecific individuals occupying the two habitats.

Imagine now that a second species, with a distinct preference for habitat B, co-exists with species 1. Assume, for the moment, that each species occupies only its preferred habitat (distinct habitat preferences; Rosenzweig, 1981). The effect of species 2 can be modelled as

$$N_{1A} = C + \delta N_{2B} \tag{2}$$

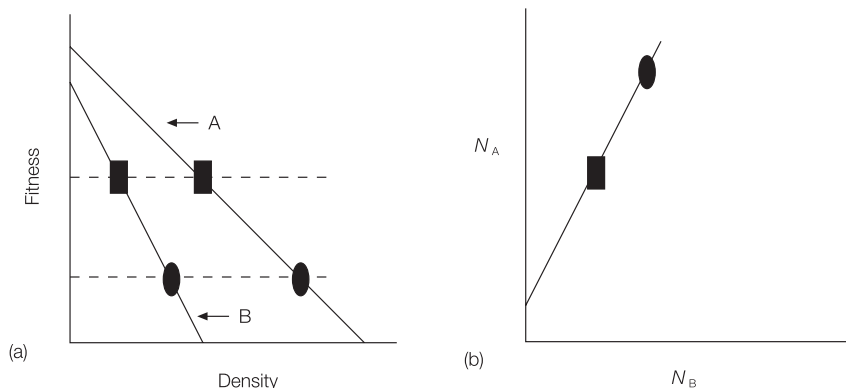


Fig. 1. An example of density-dependent habitat selection by a single species occupying two habitats, A and B. (a) The relationship between fitness and density in the two habitats. Intersections with dashed horizontal lines correspond to densities in the two habitats where expected fitness is identical in each (an ideal distribution). (b) The set of solutions to the ideal distribution is plotted as an isodar, a line of joint densities in the two habitats along which the expected fitness in each habitat is identical in both.

Equation (2) is (for the case where N_2 is absent from habitat A) the absolute or 0% isoleg of species 1, the set of joint densities that separate use of the preferred habitat only from the occupation of both habitats (Rosenzweig, 1979, 1981; Brown and Rosenzweig, 1986; the equation assumes that densities are calculated separately for each habitat). The slope represents the average per capita reduction in fitness of individuals of species 1 in habitat B caused by species 2 relative to the same effect caused by conspecific individuals. The intercepts of the isodar and the absolute isoleg are identical. Similarly, the isodar and absolute isoleg for species 2 are given as

$$N_{2B} = C' + b' N_{2A} \equiv N_{2A} = N_{2B}/b' - (C'/b')$$

and

$$N_{2B} = C' + \delta' N_{1A} \equiv N_{1A} = N_{2B}/\delta' - (C'/\delta')$$

respectively (the equivalent terms on the right-hand side allow both species' isodars and isolegs to be plotted on the same graph; see Figs 2 and 3).

I illustrate these effects in Fig. 2. Each species has a separate preferred habitat. As the density of the competing species increases, fitness is reduced in the less-preferred habitat. The reduction of fitness caused by the competitor forces the isodar intercept to increase with increasing competitor density.

The absolute isoleg is a plot of the value of the isodar intercept as it increases with competitor density in the secondary habitat (and, as noted above, is thus scaled to the effect of conspecifics). The slope of the isoleg is the per capita reduction in fitness caused by the competitor (Fig. 3). Recall Equation (1). The slope of the isodar corresponds to the reduction in fitness in the secondary habitat caused by conspecific individuals. The difference between the isodar and isoleg slopes (e.g. $b - \delta$) thereby represents the difference between intra- and interspecific competition for habitat. Isolegs and isodars are thus a convenient graphical assay for the general principle of co-existing competitors. Competing habitat-selecting species should co-exist in stable equilibrium when intraspecific competition exceeds interspecific competition (e.g. Hanski, 1995). Stable co-existence occurs, in the distinct preference case with non-crossing isolegs, when $b > \delta$.

PARTIAL HABITAT PREFERENCES

Frequently, the densities of one or both species will vary from those of the absolute isoleg (both habitats occupied). For example:

$$N_{1A} = C + bN_{1B} + b\beta N_{2B} - aN_{2A} \quad (3)$$

and

$$N_{2B} = C' + b'N_{2A} + b'\beta'N_{1A} - a'N_{1B} \quad (4)$$

where Equations (3) and (4) represent multi-species isodars (Morris 1989). Expressed this way, competition coefficients can be calculated from the partial regression coefficients in multiple regression equations (Morris, 1989; Ovadia and Abramsky, 1995; Rodríguez, 1995). The coefficients a and β measure the competitive effects of an average individual of species 2 on habitat choice by species 1. But the slope of the absolute isoleg, δ , measures the effect of an average individual of species 2 on the choice of the preferred habitat scaled to that of an average individual of species 1. Thus, on the absolute distinct preference isoleg of

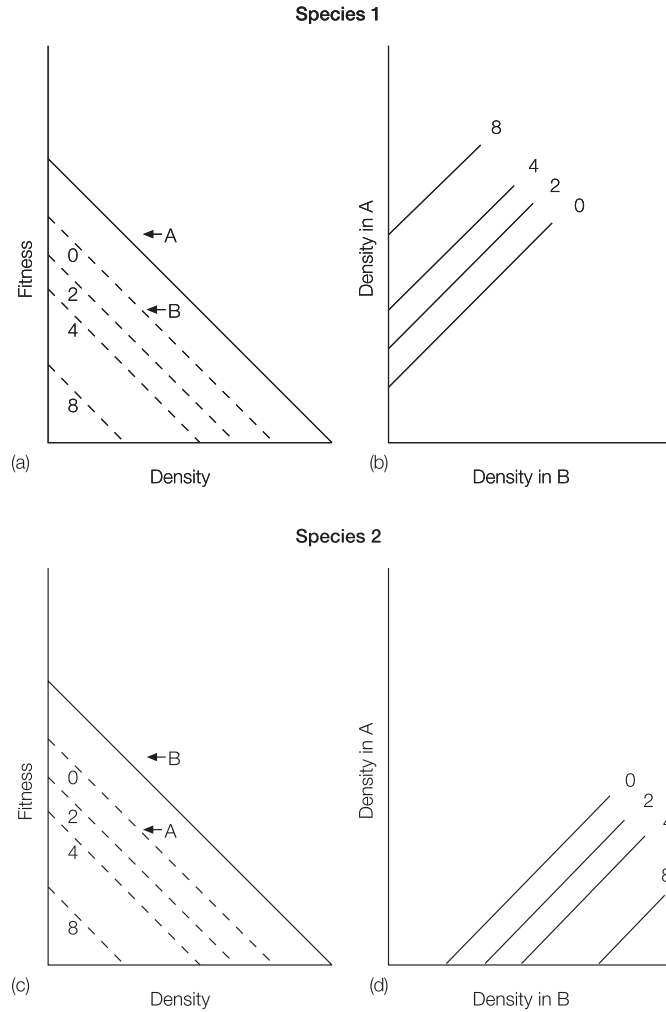


Fig. 2. An example of reciprocal effects of competing species on habitat choice. (a, b) The effect of species 2 on species 1; (c, d) the effect of species 1 on 2. Species 1 has a distinct preference for habitat A, whereas species 2 prefers habitat B. (a) The reduction in fitness of individuals of species 1 in its preferred (A) and less-preferred (B) habitats. The expected fitness of species 1 in habitat B is reduced by increased density of the competitor (numbers), which, in this example, occupies only its preferred habitat (B). (b) The respective isodars that would be created at various densities of the competitor. The isodar intercept increases with increased competitor density. (c, d) The same effects with respect to species 2.

species 1, $N_{1B} = 0$, $N_{2A} = 0$ and $\delta = b\beta$ (from Equation 3, the solution does not apply to the state space where both species co-occupy both habitats). The isoleg can be calculated directly from the isodar solution.

The region of the isoleg graph where both habitats are occupied by species 1 is filled by isolegs corresponding to the proportional use of each habitat (e.g. Pimm *et al.*, 1985). I refer to these isolegs as representing different partial preferences. Readers are cautioned that my

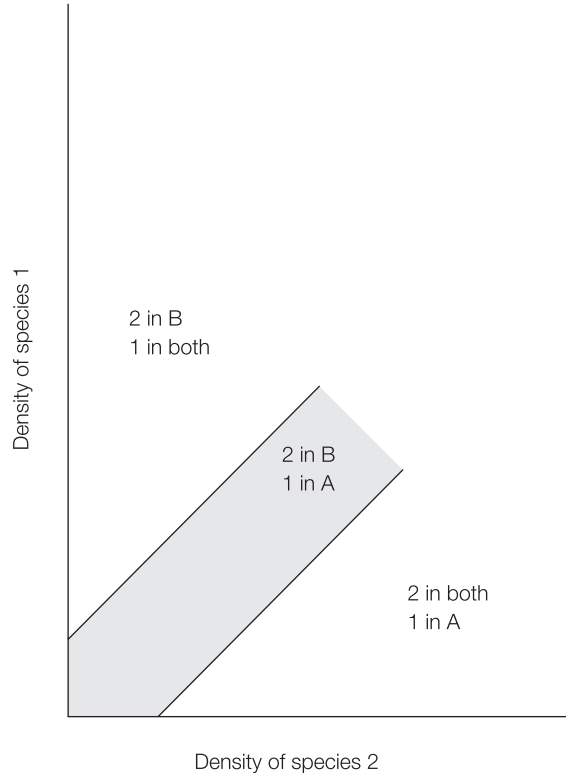


Fig. 3. Isolegs created from density-dependent habitat selection of two species with distinct habitat preferences, as shown in Fig. 2. Linear isogones assume that the per capita effect of competitors is constant. The isogone would be curvilinear or non-linear if the per capita effect depends on competitor density. The stippled area corresponds to the ghost region (each species in a separate habitat).

use of 'partial habitat preference' refers to the proportional occupation of habitats, not the differential acceptance of patches as in earlier models (Brown and Rosenzweig, 1986). Figure 4 illustrates the solution. Figure 4(a) plots fitness-density curves for species 1 as a function of variable density of its competitor, species 2, which is assumed to occupy habitat B only (as it would in the northwest quadrant of the isogone graph). Each density of species 1 along the fitness curve where species 2 is absent corresponds to a different point along its isodar, a different partial preference.

Dotted lines represent the reduced fitness in habitat B caused by different densities of the competitor (2 and 4 individuals in this example). The appropriate proportional isogone can be drawn by finding equivalent sets of proportional densities of species 1 in the two habitats at zero and correspondingly higher densities of the competitor. I illustrate these solutions for four different partial preferences of species 1 (proportion of individuals in habitat B) in Fig. 4(a). The intersections of the horizontal lines of each four-sided polygon with the fitness curves correspond to identical partial preferences (dashed lines correspond to zero density of species 2). These solutions are plotted as isogones in Fig. 4(b). Proportional isogones for species 1 rotate counter-clockwise from its absolute isogone. Parallel arguments cause those of species 2 to fan clockwise from its absolute isogone. The intercepts and slopes of

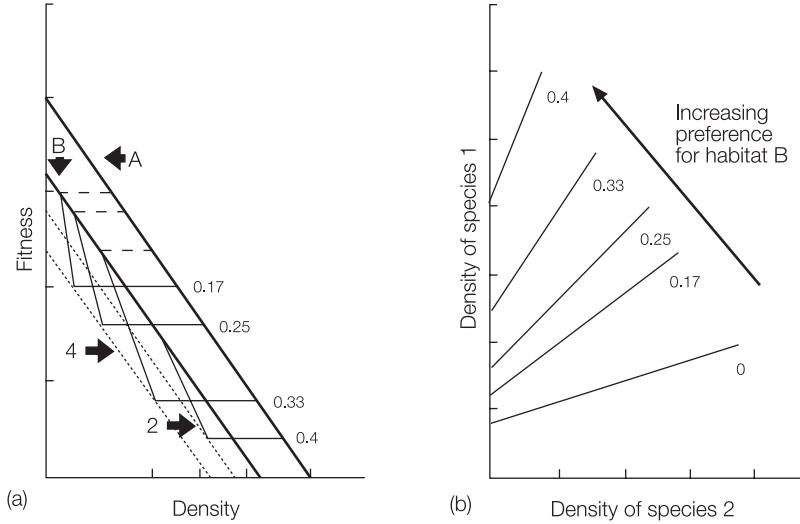


Fig. 4. (a) Fitness-density functions (solid bold lines) for a habitat-selecting species (1) with a distinct preference for habitat A in the presence and absence of a competitor (species 2) with a distinct preference for habitat B. The negative effect on species 1’s fitness of one individual of species 2, in this example, is one-half that of an individual of species 1. Dotted lines correspond to the fitness curves of species 1 in habitat B when 2 and 4 individuals (large numbers) of species 2 are present in that habitat. Solid thin lines connect fitness curves in the presence of species 2 that yield the same proportional use of the two habitats by species 1 when species 2 is absent (dashed lines). Small numbers correspond to the proportion of individuals of species 1 that occupy habitat B (different partial preferences). (b) The solutions from the fitness-density graph plotted as proportional isolegs for species 1. Numbers correspond to the same partial preferences as in (a). Note that both the intercept and slope of the isoleg increase as species 1 becomes less and less specialized on its preferred habitat (A). Similar solutions apply to any set of fitness-density functions.

each species’ proportional isolegs vary as the species becomes less and less specialized in habitat.

CONVERSION FROM ISOLEGS TO ISOCLINES

What is the magnitude of competition? Recall that habitat A for species 1 is devalued by aN_{2A} and habitat B is devalued by $b\beta N_{2B}$. The isocline coefficient, for a given density of the two species, will be the average of a and β weighted by the proportion of the two populations involved in competition. The isocline competition coefficient for species 1 is, therefore:

$$\{(N_{1A}/[N_{1A} + N_{1B}])(N_{2A}/[N_{2A} + N_{2B}])a\} + \{(N_{1B}/[N_{1A} + N_{1B}])(N_{2B}/[N_{2A} + N_{2B}])\beta\}$$

In the ghost region, $N_{1B} = N_{2A} = 0$, as does competition. The isoclines in this region are thus given by $N_{1A} = C$ and $N_{2B} = C'$ for species 1 and 2, respectively. Constant habitat-dependent competition coefficients (a and β) have driven the isolegs apart to create regions of zero habitat overlap that warp competitive isoclines to become perpendicular (the ghost of competition).

What about the rest of the isocline? Consider, first, the northwest quadrant of the graph where species 2 occupies habitat B only. The average competitive effect of species 2 on

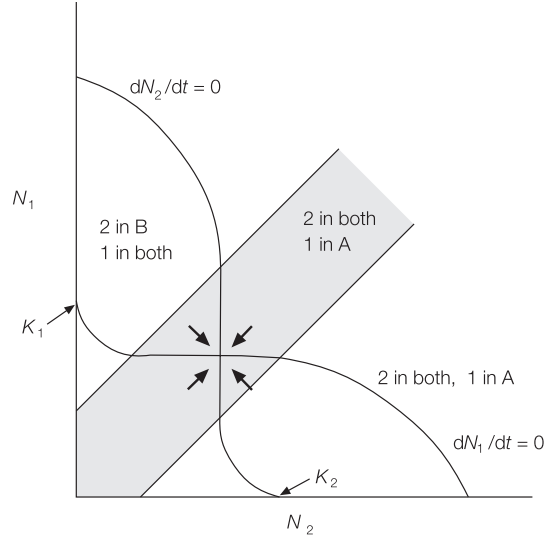


Fig. 5. An example of distinct preference isolegs for species 1 and 2 and their associated non-linear isoclines created by density-dependent habitat selection. The graph is drawn such that the point of stable two-species co-existence occurs in the ghost region (arrows, each species occupies a separate habitat).

species 1 will depend on the degree of habitat overlap. Overlap increases away from the ghost region as one crosses more and more of species 1's proportional isolegs. The isocline for species 1, in this region, will be concave away from the origin (Fig. 5). Its slope will equal the proportion of the population of species 1 living in habitat B multiplied by the competitive effect with the members of species 2 occupying that same habitat:

$$\{(N_{1B}/[N_{1A} + N_{1B}])(N_{2B}/[N_{2A} + N_{2B}])\beta\}$$

But in the northwest quadrant, species 2 occupies habitat B only and thus the isocline slope equals $\{(N_{1B}/[N_{1A} + N_{1B}])\beta\}$.

Now consider the southeast quadrant to the right and below the absolute isoleg of species 2. Species 1 occupies its preferred habitat only; species 2 occupies both. The maximum competitive effect of species 2 on species 1 is a . The proportion of individuals of species 2 occupying habitat A increases with each successive proportional isoleg. The competitive effect with species 1 $\{(N_{1A}/[N_{1A} + N_{1B}])(N_{2A}/[N_{2A} + N_{2B}])\alpha = \{(N_{2A}/[N_{2A} + N_{2B}])\alpha\}$ at any given density of species 1 will increase with each individual of species 2, and species 1's isocline will be concave towards the origin (Fig. 5). Parallel arguments apply to species 2.

Thus, for habitat-selecting species, the ghost of competition exhibits an effect and exists in varying degrees of apparition throughout the entire state space of species density. A manipulation experiment that does not control for habitat, regardless of the densities it uses, will give a different value for the average competitive effect than an experiment that restricts both species to a single habitat. This problem is overcome by the use of isodar estimates of competition.

Isodars include the actual values of a , β and δ . The isoclines plot the average competitive effects at different densities of the interacting species. At first glance, the choice of an estimator for competition would seem to depend on our intended purpose. If we wish to

know the magnitude of competition at a particular density of each species under natural conditions, we would probably want to measure the slope of the isocline. If we wish to know whether the two species can stably co-exist, we would probably wish to measure the isodar. But if we can measure the isodar, we can generate the isoclines, and we can use the weighted averages of the isodar coefficients to measure the slopes of the isoclines at all densities. Thus, we can infer the degree of competition throughout the state space of co-existence. For those species where isodars apply, isodars make field measures of isoclines redundant; costly isocline experiments may themselves become ghosts of competition past.

SHARED HABITAT PREFERENCES

If two species are most efficient in the same habitat, their competition will often be resolved by the dominant species excluding the subordinate species from the jointly preferred habitat (Pimm and Rosenzweig, 1981; Pimm *et al.*, 1985; Rosenzweig, 1985). Figure 6 illustrates the conversion from the fitness curves of the subordinate species to its absolute and proportional isoclines. At low density, all individuals, regardless of which species they belong to, can live in the preferred habitat (A). At high density, species 1 is completely excluded from the preferred habitat, and the two species do not compete because they occupy separate habitats. The zone between the two absolute isoclines is filled by species 1's partial preferences (Fig. 6), which fan out from the density where the dominant species completely excludes the

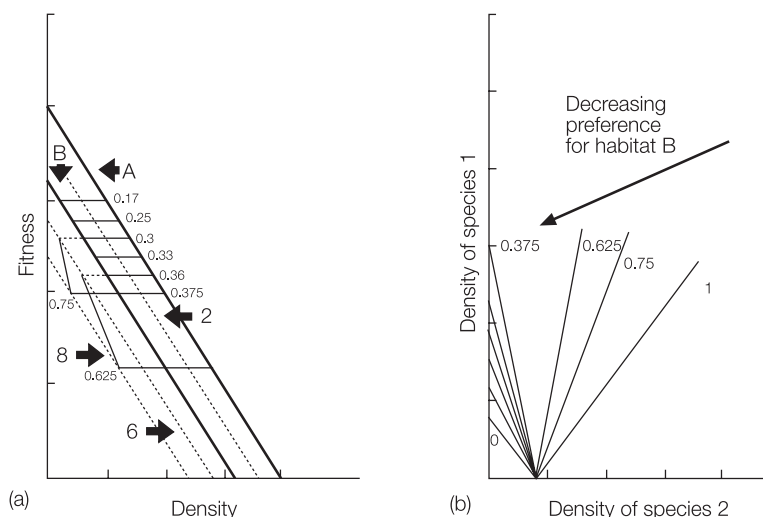


Fig. 6. (a) Fitness-density functions (solid bold lines) for a subordinate species (1) in the absence and presence of a dominant species (2) that shares a preference for habitat A. Dotted lines correspond to the fitness curves of species 1 in habitat A when 2, 6 and 8 individuals (large numbers) of species 2 are present in that habitat. Solid bent lines connect fitness curves in the presence of species 2 at high density that yield the same proportional use of the two habitats by species 1 when species 2 is at lower density (short horizontal dotted lines). Small numbers correspond to the proportion of individuals of species 1 that occupy habitat B (different partial preferences). (b) The solutions from the fitness-density graph plotted as proportional isoclines for species 1. Numbers correspond to the same partial preferences as in (a). Similar solutions apply to any set of fitness-density functions.

subordinate from the preferred habitat. In this case, however, increased preference of the subordinate species for the lower quality habitat rotates clockwise.

Species 2 may, if sufficiently specialized on habitat A, have no isoleg at all (Rosenzweig, 1985). As before, the proportional isolegs warp the isoclines of both species (Fig. 7). Figure 7 has been drawn as though species 1 (subordinate) has a negative effect on the dominant species 2. This need not be the case. Species 2 may simply exclude species 1 from the preferred habitat with no reciprocal competitive effect (near vertical isocline for species 2 when species 1 is abundant; dotted line in Fig. 7). Species 1 may, nevertheless, exert a negative effect on species 2 in its secondary habitat (if species 2 can use it at all). Then the dominant's isocline would appear concave outward (Fig. 7).

THE SCALE OF HABITAT PREFERENCE

Whether one can find absolute habitat preferences depends on the spatial scale of habitat selection, the scale of habitats in the landscape and the scale of the field design. Consider the extreme case where two habitats exist as small patches such that many occur within the typical activity range of a single forager. Each forager is likely to encounter multiple patches

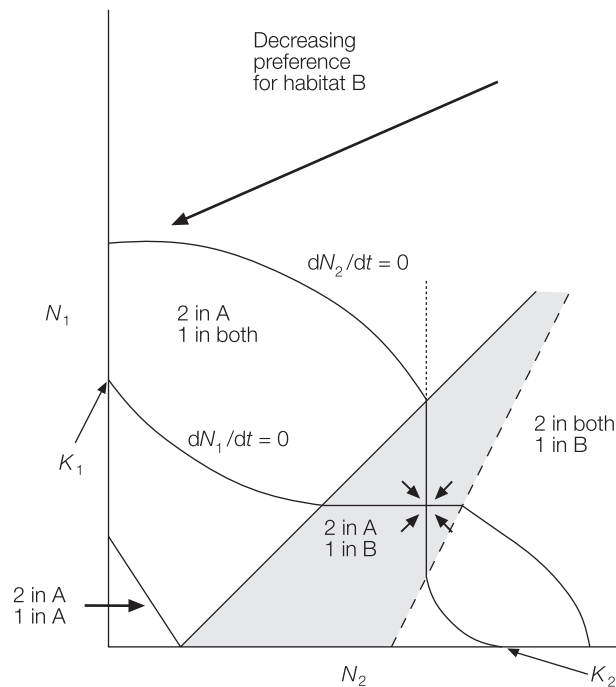


Fig. 7. An example of shared preference isolegs and their non-linear isoclines. The isolegs for the subordinate species (1) are drawn as solid lines and the isoleg of the dominant species (2) is drawn as a dashed line. The dominant's isocline assumes that the subordinate has an exploitative effect on the dominant species. Arrows indicate stable competitive co-existence in the ghost region. The dotted line represents a possible vertical-to-concave dominant isocline where the dominant is capable of excluding the subordinate from the preferred habitat with no reciprocal competitive effect.

of each habitat during any foraging bout (fine-grained habitat use; MacArthur and Levins, 1964). Unless foraging individuals can instantly recognize the patches and avoid them without any loss in foraging efficiency (an unlikely scenario), each will be used, even at low density. There will be no absolute habitat preference and no absolute isoleg.

I illustrate one way of modelling such fine-grained habitat use in Fig. 8. Species 1 has a distinct preference for habitat A, but all individuals must use both habitats at all densities. Both habitats will be used by a density-dependent habitat selector at low density only if the fitness curves share a common intercept (the isodar necessarily passes through the origin). Dashed lines in Fig. 8 model the effect of a second fine-grained species with a preference for habitat B. The preferential use of B by species 2 increases the per capita reduction in fitness in that habitat by species 1 (this is necessarily true because both habitats are always occupied by members of each species, so the fitness curves must maintain a common fitness intercept).

Each additional individual of the competitor thus creates a unique vertical proportional isoleg for species 1 (Fig. 8b) (whenever a linear isodar passes through the origin, the relative abundance of individuals in the habitats is constant; Morris, 1990, 1994). Parallel arguments produce horizontal isolegs for species 2. Note that maximum habitat overlap occurs, as at the coarse-grained scale, in the northwest and southeast quadrants of the density state space. The isoclines are warped, but never become perpendicular because there is no region where either species can express an absolute habitat preference.

Shared preferences can be modelled similarly (Fig. 9), but yield dramatically different and more potential kinds of isoclines. Competition is low in the northwest and southeast quadrants because both species reduce their preference for habitat A with increased com-

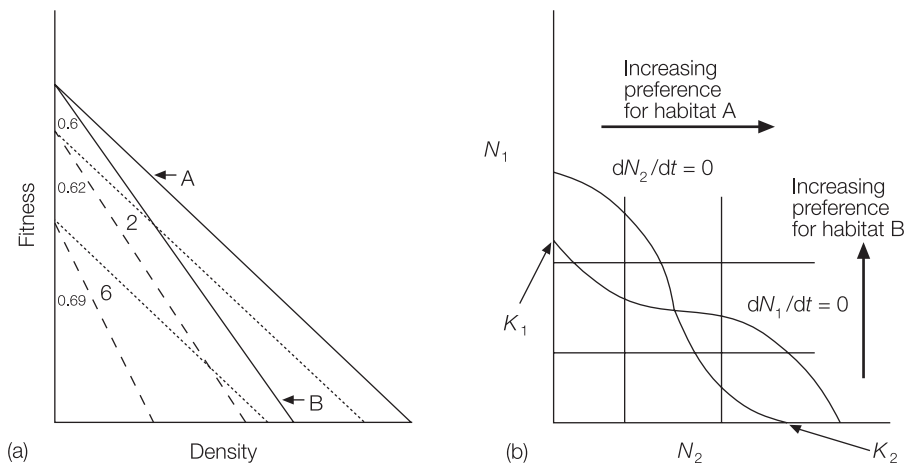


Fig. 8. (a) Fitness-density functions for species 1 in habitats A and B in a fine-grained environment where it uses both habitats at all densities. Dashed and dotted lines represent the reduction in fitness caused by species 2 that is assumed to have a distinct preference for habitat B. All possible densities of species 1 yield identical partial preference (small numbers, proportion of individuals occupying habitat A) for any given density of species 2 (large numbers). Parallel arguments apply when species 2 is the target species. (b) The resulting isolegs and isoclines. The isolegs for species 1 are vertical and those for species 2 are horizontal.

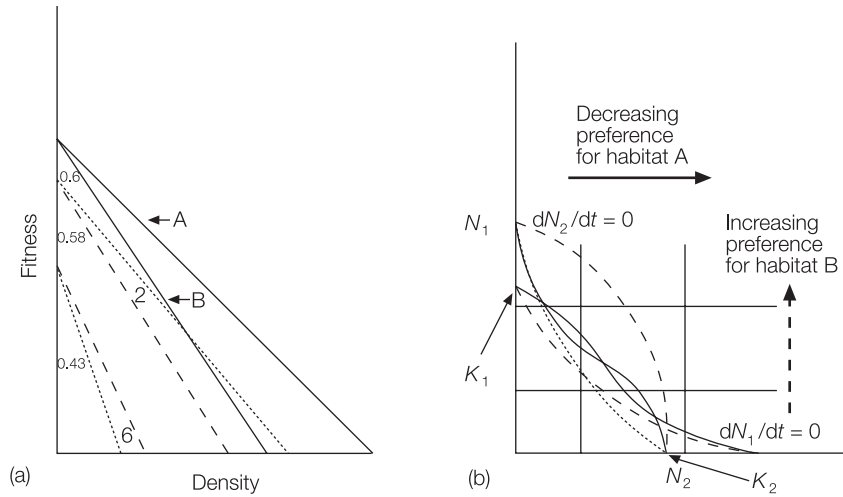


Fig. 9. (a) Fitness-density functions for species 1 in habitats A and B in a fine-grained environment where it uses both habitats at all densities. Dashed and dotted lines represent the reduction in fitness caused by the dominant species 2 that is assumed to share a preference for habitat A. All possible densities of species 1 yield identical partial preference (small numbers, proportion of individuals occupying habitat A) for any given density of species 2 (large numbers). Parallel arguments apply when species 2 is the target species. (b) The resulting isogons and isoclines. The isogons for species 1 are vertical and those for species 2 are horizontal. Three sets of isoclines are displayed. Solid curved lines reflect low competition in the northwest and southeast quadrants where habitat overlap is minimized (they create the opportunity for locally stable equilibria of species co-existence). Dashed curves represent isoclines where species 1 has no effect on habitat use by the dominant species 2 (species 2 has no competitive isogon; bold dashed arrow). The dotted species 2 isocline is an example of what may apply when dominance is restricted to the preferred habitat A. Species 1 has little interspecific competitive effect even at high density in habitat A. With increasing density of the dominant, species 1's preference for habitat A declines. The average competitive effect on species 2 increases because there is increased overlap in the habitat (B) where species 2 cannot express its dominance over species 1 (concave isocline).

petitor density. The resulting isoclines can produce two locally stable equilibria of species co-existence.

When species 2 is highly specialized on habitat A, it may be unable to exploit habitat B and will lack competitive isogons (species 1 has little effect on habitat use by species 2; bold dashed arrow in Fig. 9b). The intensity of competition would depend on species 1's isogon only; competition declines with increased density of species 2 (dashed isoclines in Fig. 9). In some cases, dominance may occur in only the jointly preferred habitat (e.g. aggressive neglect; Brown, 1971). If species 2 is sufficiently dominant in that habitat, competitive effects of species 1 on species 2 would be low when the density of the dominant is low (most individuals of species 1 occupy habitat A where it has little effect on the dominant species) and increase with higher densities of the dominant (more overlap in habitat B where species 2 cannot avoid competition by dominance). The isocline would be concave away from the origin (dotted line in Fig. 9b).

Now consider the polar alternative where patches of each habitat exceed the typical foraging ranges of individuals. Only those individuals that locate their foraging ranges near

the boundary between habitats will have the opportunity to exploit both. At low density, habitat selectors should occupy only the better habitat (absolute preference).

Species are likely to exhibit both scales of habitat use in hierarchical landscapes. Species that can use a variety of habitats will, at some scale, perceive habitats as coarse-grained (e.g. prairie/badland or mesic/xeric forests exploited by deer mice; Morris, 1992, 1996b). Species will probably perceive smaller patches as fine-grained within the coarse-grained habitat mosaic. Competitive co-existence could occur at either, and possibly both, scales. If habitat selection occurs at both scales, the isodar coefficients will vary with the nested pattern of habitat use (the habitats are different at the two scales, so the isodars must be also).

ISODAR ESTIMATES OF COMPETITION

Equations (2) and (3) demonstrate that one should be able to estimate habitat-dependent competition coefficients from isodars. The technique has been applied, with apparent success, to co-existing rodents (Morris, 1988, 1989) and to salmonid fishes (Rodríguez, 1995). In both cases, isodar analysis revealed the true habitat preferences of each species, as it did for co-existing gerbils in Israel (Ovadia and Abramsky, 1995). The gerbil isodars were criticized, however, because they appeared incapable of revealing interference competition that serves as the main mechanism of gerbil co-existence (Ovadia and Abramsky, 1995).

Large and dominant *Gerbillus pyramidum* concentrates its foraging before midnight, whereas the smaller, subordinate *G. allenbyi* delays foraging until *G. pyramidum* is mostly inactive (Kotler *et al.*, 1993; Ziv *et al.*, 1993). The interference should produce significant higher-order interactions in the isodars if interference intensifies with the density of competitors (Morris, 1989; Ovadia and Abramsky, 1995). Despite several attempts, none of the gerbil isodars included a higher-order effect. One interpretation is that the theory is unreliable. Another interpretation is more positive: while it often makes sense to assume that interference itself is density-dependent, the gerbil isodars refute the assumption and illustrate that some forms of interference are likely to produce only additive effects. The dominance asymmetry between *G. pyramidum* and *G. allenbyi* may be either so great, or be complemented by relatively inefficient foraging by the dominant species (Kotler *et al.*, 1993), that the best strategy for *G. allenbyi* is simply to avoid *G. pyramidum*.

DISCUSSION

How well do current data fit the predictions of the isodar/isoleg theory? At least two studies have documented fine-grained habitat selection with partial preferences. Three species of hummingbirds varied their partial preference for rich habitats with changing densities of competitors (Pimm *et al.*, 1985). The same pattern emerged from studies of two gerbil species occupying stabilized sand versus semi-stabilized dune habitats in the Negev Desert (Abramsky *et al.*, 1990). In each case, any given forager was likely to visit multiple patches of each habitat.

Predictions of absolute preferences in large-scale patches have been confirmed by studies of small rodents occupying adjacent habitats in a variety of ecosystems. Morris (1996b) examined habitat selection of rodents occupying xeric and mesic forest habitats on different mountains and was able to draw the complete isodars and absolute isolegs for the two most common species. Deer mice preferentially occupied xeric sites and tended, at low-density locations, to be absent from nearby mesic forest. Red-backed voles preferred mesic forest

and were absent, at low density, from nearby xeric sites. The isodars had higher slopes than the nearly perpendicular isolegs. The two species co-exist without competition because each has a distinct preference for the alternative habitat. Partial preferences for the secondary habitat necessarily increased away from the absolute preference isoleg because there was no detectable interspecific competition for habitat; the proportional occupation of the preferred habitat decayed with increased density along the linear isodars. Absolute preferences have also been observed for deer mice occupying badland and prairie habitats in southern Alberta (Morris, 1992), and for red-backed voles in beach-ridge and wetland habitats along the coasts of Hudson Bay and James Bay in northern Ontario (Knight and Morris, 1996).

Abramsky *et al.* (1991, 1992, 1994) drew the isoclines of two gerbil species occupying stabilized sand versus semi-stabilized dune habitats in the Negev Desert. *Gerbillus allenbyi* and *G. pyramidum* shared a preference for the semi-stabilized dunes with isodar intercepts greater than zero (Ovadia and Abramsky, 1995). Theory predicts that the subordinate *G. allenbyi* should face intense competition in the northwest and southeast quadrants of the two-species state space, with little competition in the ghost region (the isocline should possess an inflection point; Fig. 7). The isocline of *G. allenbyi* obeyed the prediction.

The isocline of *G. pyramidum* was concave away from the origin (relatively high competition in the southeast quadrant where it overlapped with *G. allenbyi* in semi-stabilized dunes; low competition in the northwest quadrant). As pointed out above, this shape will occur when the subordinate species has little competitive effect on the dominant, and especially so when dominance is linked to the jointly preferred habitat. Both species are more efficient foragers in patches surrounded by semi-stabilized dunes (better escape substrate from predators; Ziv *et al.*, 1995). Is it possible that the concave *G. pyramidum* isocline reflects a similar substrate effect on interspecific dominance?

Current data thus suggest that species co-existence is often predicated on differential habitat use that creates the ghost of competition. The linear isodars for rodents also suggest constant habitat-dependent competitive effects that should allow us easily to calculate the average competitive effect (isocline slope) at any density.

Which competition coefficient is the reliable one? The answer depends on the purpose of the study. If the intent is to determine the per capita effect of individuals of one species on those of another, isodars are the preferred option. Isodars also let us infer whether co-existence is stable or not (intraspecific competition exceeds interspecific competition).

The average coefficient in both habitats should be used by those who wish to draw the competitive isoclines to determine the actual point about which competitive co-existence should regulate population densities. Even this can be accomplished by isodar analysis. Once we know the true habitat-dependent competition coefficients, we can plot the isoclines using real data on the relative densities of each species occupying the two habitats.

Some may question the applicability of a theory dependent on paired habitat comparisons when many species are likely to recognize and respond to more than two habitat classes. The problem may be more abstract than real. Whereas it is possible for a large number of habitats to converge on a single point, it is unlikely that landscapes lack much simpler boundaries between pairs of habitats where habitat selection and potential competitive effects can be assessed (e.g. Morris, 1992; Knight and Morris, 1996). Moreover, the habitat problem is not restricted to isodars. Any estimate of competitive interaction is sensitive to sampling, and especially so to the variety of habitats included in the estimate. We would do well to keep in mind that competing species do not resolve their interactions on the basis of our average estimates of their regional, or even local, competitive effects.

Competition is resolved at the scale of individual interactions, and it is at that scale where one would normally use isodars to estimate habitat preferences and competition.

The conditions I outline for the stable co-existence of species with distinct habitat preferences allow isolegs to converge, or even to intersect. When they do so, the absolute isoleg must simultaneously account for the effect of the competitor in the alternative habitat [where it inflates the density of the target species in habitat A (a positively sloped isoleg)] as well as its effect in the same habitat [where it reduces the density of the target species in habitat A (changes the isoleg slope)]. The isolegs deflect one from the other and magnify the zone where both species may co-occupy both habitats.

Recall that the proportional isolegs rotate in opposite directions. In the zone where both habitats are occupied, reduced overlap in habitat A will tend to be countered by increased overlap in B. Competition will be most intense in the northwest and southeast quadrants where one species only is restricted to its preferred habitat. The isoclines will be warped but never become perpendicular.

How does one reconcile crossed isolegs with Brown and Rosenzweig's (1986) proof, using models of optimal patch use, that distinct preference isolegs for two competing species should never intersect? Brown and Rosenzweig's proof assumed that species consume identical resources within a habitat and that the resources found in different habitats are perfect substitutes. Each species is able to harvest resources to a lower level in the preferred habitat than in the secondary one. At equilibrium, species 1 can use both habitats only if the resource density in the secondary choice (habitat B) is greater than that in the preferred habitat A. This can never occur if the competitor is also present in both habitats because its conditions for the joint use of the two habitats are a mirror image of those for species 1 (species 2 requires greater resource density in habitat A than in habitat B).

It is instructive to think of Brown and Rosenzweig's proof in the context of each species' isocline within one or the other habitat. Species 1 can competitively exclude species 2 from habitat A; the isocline for species 1 in habitat A lies above that for species 2. Species 2 competitively excludes species 1 from habitat B in which the isocline for species 2 lies above that for species 1. The composite isoclines necessarily cross perpendicular to one another in the region where each species is restricted to a different habitat. The resulting ghost will be revealed by an isodar analysis because the interspecific effect in a shared habitat exceeds intraspecific competition.

Intersecting isolegs (at least for cases where the isodar slope ≥ 1 , and even for many with slope < 1) imply the alternative of stable co-existence within habitats because intraspecific competition is greater than the interspecific effect. The isoclines will cross in the region where both habitats are occupied. The underlying isodar theory makes no explicit assumptions about identical diets or the substitutability of resources among habitats.

Isodar theory does assume that the mechanism of competition is mediated via density-dependent habitat selection. This would appear to be necessarily true for exploitative competition. Interference is also likely to be expressed via habitat (shared preference). Apparent competition for predator-free space (Holt, 1977, 1984; Jeffries and Lawton, 1984; Holt and Lawton, 1994) implicitly assumes habitat selection as well (e.g. Martin, 1996), which could be difficult to distinguish from pure competitive effects. Apparent competition is a universal complication in the assessment of interspecific competition, and similar to the difficulties associated with habitat, not one restricted to isodars.

Differential habitat use and isodars may not always apply to situations where species partition time rather than space [e.g. species capitalizing on a trade-off between the ability

to forage efficiently at high versus low resource density (Kotler *et al.*, 1993) – but such a mechanism may often induce a strong spatial component between rich and poor patches; or species that co-exist via a trade-off between travel costs versus foraging efficiency (Brown, 1989)], although they may often produce shared preferences. Regardless, the theory applies to enough mechanisms that it should often capture the competitive dynamics of many species.

We need definitive experiments similar to those of Abramsky *et al.* (1991, 1992, 1994) to test the theory. Experiments must be designed and interpreted carefully so that it is clear which competition coefficient is being estimated at each step. Even so, we should not be surprised to find conditions where isodars give biased estimates of competitive interaction. Linear isodars may underestimate the intensity of competition, for example when the state of individual competitors varies with density. If individuals tend to be in a poorer state at high as compared to low density, their per capita competitive effect is likely to be reduced. The linearity assumption is not crucial to application of the theory. Density-dependent shifts in competitive effect should produce curvilinear or non-linear isodars whose solution would correctly map density-dependent competitive effects. Pre-emptive habitat selection, for example, often bends isodars into curvilinear and non-linear forms (Morris, 1994). Non-linear isodars complicate the analyses, but the essential linkages between isodars, isolegs, isoclines and the ghost of competition will remain. The key point is that the competitive ghost can be revealed by isodar analysis.

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