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A HAUNTING LEGACY FROM ISOCLINES: MAMMAL COEXISTENCE AND THE GHOST OF COMPETITION

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Many of our concepts about species coexistence are rooted firmly in the analysis of competitor isoclines whose slopes estimate the average magnitude of competition. Realistically, competition will vary among habitats, and habitat selection will be a major contributor to coexistence. Competition will vanish to zero (the ghost of competition) when species occupy completely separate habitats, even though the potential for competition remains high. Competitive potential can be estimated from slopes of absolute isolegs that define boundaries between specialized use of a single habitat and the joint occupation of one or more additional habitats. Interpretations of current theories suggest, however, that we may seldom be able to plot isolegs because they represent a wall of competition that species seldom cross. If so, isoclines bend sharply at the isoleg, and population dynamics are restricted to the ghost region. But when competition is resolved by habitat selection, isoclines bend gradually, and the wall of competition disappears. The isolegs become visible through analysis of habitat isodars, lines that represent the set of each species' density such that expected fitness is equivalent in each occupied habitat. Preliminary analyses of rodent isodars agree with theory, reveal the ghost, and confirm a central role for density-dependent habitat selection in competitor coexistence.

Key words: *Clethrionomys, Dicrostonyx, Lemmus, Peromyscus,* competition, habitat selection, isocline, isodar, isoleg

Isoclines and habitat selection were crucial to Robert MacArthur's approach to geographical and community ecology. MacArthur used isoclines to illustrate competitive coexistence (MacArthur, 1972), to explore use of patchy environments (MacArthur and Levins, 1964), and to develop theories of consumer-resource dynamics (MacArthur, 1972; MacArthur and Levins, 1964). Habitat selection was central to MacArthur's initial theories of optimal patch use (MacArthur and Pianka, 1966), his appreciation of source-sink dynamics (MacArthur, 1972), and species diversity (MacArthur, 1964; MacArthur and MacArthur, 1961), and mechanisms of competitive coexistence that he made famous (MacArthur, 1958; MacArthur and Wilson, 1967).

Those familiar with MacArthur's legacy might have anticipated that the joining of isoclines with habitat selection would yield fundamentally new insights into species coexistence. They have not been disappointed. The differential habitat selection by competing species warps isoclines and causes competition, like a ghost, to vanish (Rosenzweig, 1974, 1979, 1981, 1985, 1991). Thus, we face a disturbing paradox of coexistence. We cannot measure competition that is responsible for habitat segregation because the species occupy separate habitats.

I search for a solution to the paradox by first reviewing the ghost of competition and its implications to habitat selection and competitive coexistence. I demonstrate how one can use theories of optimal habitat selection to reveal competitive ghosts and illustrate the solution with data on habitat use by coexisting rodents. I conclude by noting how these solutions reflect an exciting new paradigm that uses the optimal behaviors of individuals to deepen our understanding of population dynamics and community structure. The origins of the paradigm permeate MacArthur's perspectives on geographical ecology.

THE GHOST OF COMPETITION

Rosenzweig (1974, 1979, 1981, 1985, 1991), in a series of elegant and provocative papers, demonstrated how habitat selection between competing species can eliminate the competition between them. The explanation assumes that individuals occupy habitats in a way that maximizes their fitness and, across a reasonable range of densities, fitness declines with the increased density of each species (Fretwell and Lucas, 1970). Below some threshold set of their joint densities members of each species should selectively occupy only a single habitat, beyond that threshold the population will be generalized using that habitat and at least one other. The boundary between selective versus generalized habitat use defines the absolute isoleg of the population (Morris, 1999; Rosenzweig, 1974, 1979, 1981, 1991; Fig. 1).

Isoclines will frequently cross in the zone between isolegs where each species occupies a separate habitat (the ghost of competition). Stable competitive coexistence occurs when species are segregated spatially. But species that have no spatial overlap cannot compete directly with one another, and isoclines are warped to intersect at right angles (Fig. 1a). The competition responsible for habitat selection is invisible because of it.

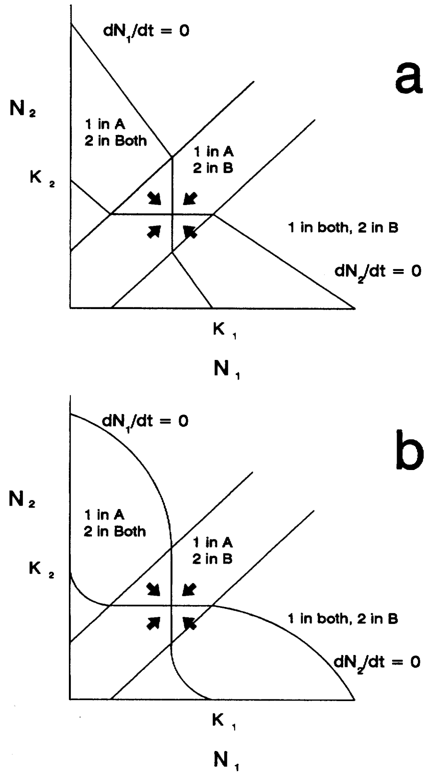

FIG. 1.—a) Absolute isolegs (positively sloped lines) and their associated isoclines (negative slopes) that illustrate the paradox of coexistence for a pair of habitat-selecting competitors with distinct habitat preferences. The isoclines are kinked, bending sharply and discretely at the isoleg. Competition is zero near the point of stable competitive coexistence because each species occupies a separate habitat (after Brown and Rosenzweig, 1986). b) The solution to the paradox for a pair of habitat-selecting competitors with distinct habitat preferences. Perpendicular isoclines in the ghost region bend continuously away from the isolegs. Mean competition increases gradually toward maxima where one species is abundant in its preferred habitat when the density of its competitor is low (after Morris, 1999, and Rosenzweig, 1981).

Interspecific competition in this system is expressed through the habitat choices made by each species. Thus, if one could draw absolute isolegs, interspecific competition for habitat could be estimated easily from their respective slopes (Morris, 1996, 1999). The ghost of competition suggests that this may be impossible even for species whose population densities fluctuate about the jointly determined equilibrium. A common interpretation of competitive ghosts implies that isoclines are kinked, bending sharply and discretely at the absolute isoleg. Competition changes abruptly from zero on one side of the isoleg to its maximum value on the other side. Fluctuating densities that reach an isoleg bump into a wall of competition that they may be unable to cross. Species retreat into their preferred habitats, the ghost is reinforced, and we seldom expect to find the species jointly occupying one or both habitats. Without those densities, we do not know where the absolute isoleg lies, and we are unable to estimate the competitive effect. The paradox of coexistence lies not in the ghost of competition but in the competitive wall that it appears to create.

Recall, however, that isoclines measure the average competitive effect for the population as a whole. Within the ghost region, each species occupies a separate habitat and competition is necessarily zero. The isoclines are perpendicular to one another. Imagine that the population of one or both species increases so that the joint densities lie on the absolute isoleg. Any further increase will cause individuals to begin to use more than a single habitat, but those individuals will be a small fraction of the population at large (or the total amount of time spent by the population in other habitats will be a small fraction of the total). As population density increases further, a greater and greater proportion of the population will occupy other habitats where they interact with their competitor. Thus, competition increases gradually away from the isoleg (Morris, 1999; Fig 1b), and the wall of competition does not exist. Without the competitive wall, fluctuating population densities may often occur outside of the ghost region. One can draw the isoleg and measure the competitive effect.

A FORMAL TREATMENT: ISOLEGS AND ISODARS

When species occupy separate habitats the competitive effect is likely to vary with habitat. We can model such a system by expanding Lotka-Volterra-Gause competition equations. For two competing species we can denote the per capita population growth of species 1 in habitats A and B as,

$$(1/N_{1A})dN_{1A}/dt = r_{1A}([K_{1A} - \alpha_{11A}N_{1A} - \alpha_{12A}N_{2A}]/K_{1A}) \quad (1)$$

and

$$(1/N_{1B})dN_{1B}/dt = r_{1B}([K_{1B} - \alpha_{11B}N_{1B} - \alpha_{12B}N_{2B}]/K_{1B}) \quad (2)$$

where N equals number of individuals, r is intrinsic rate of natural increase, K is carrying capacity, α is a measure of competition, and subscripts denote species and habitats, respectively. If fitness is equalized between the two habitats (e.g., an ideal-free distribution—Fretwell and Lucas, 1970), equations 1 and 2 also are equalized and, keeping in mind that the intraspecific coefficients equal 1 by definition,

$$N_{1A} = \left(K_{1A}\left[1 - \frac{r_{1B}}{r_{1A}} + \frac{r_{1B}\alpha_{12B}N_{2B}}{r_{1A}K_{1B}}\right] - \frac{\alpha_{12A}N_{2A}}{r_{1A}}\right) + \frac{r_{1B}}{r_{1A}}\frac{K_{1A}}{K_{1B}}N_{1B} \quad (3)$$

Equation 3 is the isodar of species 1, the set of densities where the expected fitness in each habitat is equal (Morris, 1988, 1989, 1990, 1994, in press). Note that the competitive effects of species 2 act to increase (in habitat B) or decrease (in habitat A) the isodar intercept (the first major right-hand term; I am indebted to J. S. Brown who first showed me Lotka-Volterra isodars on the back of an envelope in a day-care center. C. Guthrie and D. Moorhead have developed, independently, a series of simulations to evaluate isodars and isolegs with Lotka-Volterra equations. The simulation approach is valuable because it should, among other things, allow us to illustrate isodars and isolegs across the entire state-space of species densities).

Imagine that the two competing species have distinct habitat preferences (e.g., Fig. 1). The equation for species 1's absolute isoleg thus becomes (setting $N_{1B} = 0$ in equation 3 because species 1 occupies only habitat A at the isoleg)

$$N_{1A} = K_{1A}\left(1 - \frac{r_{1B}}{r_{1A}}\right) + \frac{r_{1B}}{r_{1A}}\frac{K_{1A}}{K_{1B}}\alpha_{12B}N_{2B} \quad (4)$$

Note that the isoleg intercept corresponds to the isodar intercept in the absence of the competitor. The slope of the isoleg (+ve) equals the competitive effect for habitat from species 2. Note, also from equation 4, that the competitive effect varies with the ratios of the target species' carrying capacities and intrinsic growth rates in each habitat. The reason for this apparently peculiar result is because interspecific coefficients in equations 1–4 are scaled relative to the intraspecific habitat-dependent effect (the isodar slope). Thus, competition for habitat by species 2 is increased when habitat B can hold relatively few individuals of species 1 (each additional individual has a higher negative effect on fitness in that habitat than when the carrying capacity is high) and, for a given carrying capacity, it is reduced when the potential growth rate of species 1 in habitat B is relatively small (the effect of each individual is reduced because fitness is initially small).

Now imagine that the two species share a preference for habitat A (thus, in equation 3, $N_{1B} = N_{2B} = 0$). Both species occupy habitat A, the isoleg for species 1 is given by

$$N_{1A} = K_{1A}\left(1 - \frac{r_{1B}}{r_{1A}}\right) - \frac{\alpha_{12B}}{r_{1A}}N_{2A} \quad (5)$$

and the absolute isoleg has negative slope. The important result is that the slope of each isoleg, whether for distinct or shared preference, can be estimated from a multiple regression solution to the isodar (equation 3) if one has data where the species occupy both habitats.

In practice, densities used for equation 3, and those used for equations 4 and 5 will differ. When constructing an isodar, one calculates density within each habitat separately. For isolegs, the density estimate is obtained from both habitats. In equation 5, number of individuals in habitat A is the same as in equation 3, but the actual value of density will depend on the relative areas or volumes of the occupied habitat A and unoccupied habitat B included in the census. The density "correction factor" is the same for both species and has no effect on the slope of the isoleg.

TESTS OF ISODAR THEORY WITH COEXISTING MAMMALS

What kind of system would one use to test our ability to draw isolegs and measure competition from isodars? One would choose, presumably, as simple a community as possible in which similar species possess well-documented habitat preferences that may be caused by interspecific competition. I have drawn isodars and isolegs for two such systems.

Clethrionomys gapperi (southern red-backed vole) and *Peromyscus maniculatus* (deer mouse) co-occur in forest habitats throughout much of their joint geographic ranges, but their relative abundances vary throughout the habitat mosaic. Red-backed voles tend to be abundant in wet forests, deer mice are abundant in dry (Morris, 1996). Observational studies suggest that the differential use of habitat by red-backed voles and deer mice has little to do with competition (Morris, 1983; Wolff and Dueser, 1986), but experiments on islands (Crowell and Pimm, 1976) suggested a significant competitive effect.

My assistants and I censused both species in adjacent xeric and mesic-forest habitats located on different exposures at nine locations in the Rocky Mountains of southern Alberta in 1989. I analyzed the census data to infer isodars and their associated isolegs. No interaction coefficient was significantly different from zero. The resulting near-perpendicular isolegs illustrate that the distinct preference for the wetter habitat by voles, and the similar preference for drier habitat by mice, is not caused by competition (Morris, 1996; Fig. 2). Crossed isolegs always yield a region where each species occupies a different habitat at low density, but not necessarily a competitive ghost.

Yet, the ubiquitous distribution of *Pero-*

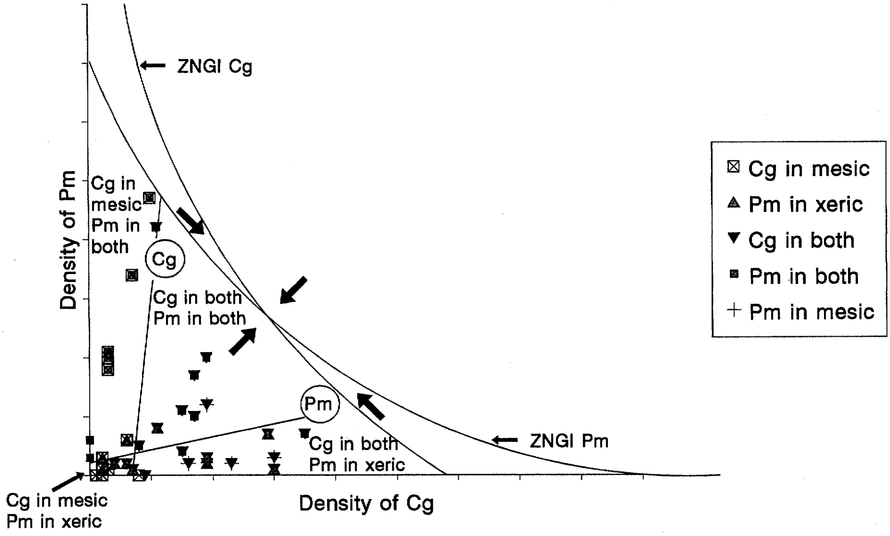

FIG. 2.—Nearly perpendicular isolegs of coexisting *Clethrionomys gapperi* (Cg, almost vertical) and *Peromyscus maniculatus* (Pm, almost horizontal) illustrate that their distinct habitat preferences are not influenced by interspecific competition. Stable isoclines (ZNGI, curved lines) can be created by habitat selecting generalist predators (after Morris, 1996).

myscus and *Clethrionomys* in northern small-mammal assemblages (Morris and Knight, 1996) suggests that their joint dynamics are not independent. Both species share numerous predators whose own prey-related habitat preferences may act to stabilize vole and mouse dynamics. Predators that concentrate on whichever species is more abundant will be more active in one habitat allowing the other species to increase when rare. Predators can thereby create stable non-competitive isoclines that reinforce the coexistence of the two species (Morris, 1996; Fig. 2).

This habitat-dependent predator response differs from the accepted ecological interpretation that the numerical response of predators to the abundant prey species will increase their predation on the less abundant species. If so, densities of the two prey species will be correlated negatively (apparent competition—Holt, 1977). Incongruously, when both predators and prey are habitat selectors, apparent competition may emerge only at those sites where densities of the prey species would be correlated positively in the predators' absence. Although the hypothesis remains untested, the insight owes its origin explicitly to the analysis of how habitat selection influences isoclines and species coexistence.

Lemmings belong to an even better community within which to search for competitive ghosts. Throughout much of their North American range, *Dicrostonyx groenlandicus* (collared lemming) and *Lemmus trimucronatus* (brown lemming) are the only abundant rodents. Brown lemmings, specializing on graminoids and moss, occupy lower and wetter sites on a moisture gradient than do collared lemmings whose diet is biased toward forbs and shrubs (Batzli et al., 1983; Krebs, 1964; Pitelka and Batzli, 1993; Rodgers and Lewis, 1986; Watson, 1956). Both species possess well-documented fluctuations of abundance (Chitty, 1996; Elton, 1942; Krebs, 1964; Oksanen, 1990; Stenseth and Ims, 1993) that should propel their joint dynamics beyond their respective isolegs.

In July 1996, Douglas Davidson and I sampled lemmings in 12 0.36-ha study plots near Walker Bay on the Kent Peninsula of Canada's Northwest Territories (Nunavut; 68°21'N, 108°05'W) when both species were at, or near, record high densities. Each plot was composed of about equal proportions of dry hummock heath and adjacent wet-sedge meadows. We determined actual proportions of the two habitats on each grid by classifying each of 25 trap stations on the basis of plant and substrate cover. We estimated densities of lemmings as the number of different animals captured per trap station in each habitat and used multiple regression to generate the respective isodars (Morris, 1989; Ovadia and Abramsky, 1995; Rodríguez, 1995). Here, I provide a preliminary summary of those analyses, including the species' isolegs. The detailed analysis and interpretation, including the calculations for the isolegs, will be published independently (Morris et al., in press).

We returned to the study area in June 1997 to obtain population estimates during a dramatic decline in abundance of lemmings. We used the 1997 data to test our inferences about the lemming isolegs and to gain new insights into lemming dynamics.

Two lemmings with distinct habitat preferences.—The isodars for the two lemming species documented a distinct preference for the wet-meadow habitat by brown lemmings ($L_W = 0.54 - 0.64\ L_WD_W$ where L and D refer to density of *Lemmus* and *Dicrostonyx* in habitat i, respectively, and where the L_WD_W interaction is based on standardized values; $P < 0.001$ for both coefficients) and a complementary preference for hummocks by collared lemmings ($D_H = 1.18 - 1.59\ L_H - 0.76\ L_WD_W$; all coefficients significant, $P < 0.05$). There was no significant effect of conspecific density in either isodar, and conveniently, each isodar equation corresponds to its respective absolute isoleg. Note, as well, that there is no direct effect of *Dicrostonyx* on density of *Lemmus* in wet habitat; the isodar for *Lemmus*, and its near-vertical isoleg, are essentially independent of density of *Dicrostonyx* (Fig. 3).

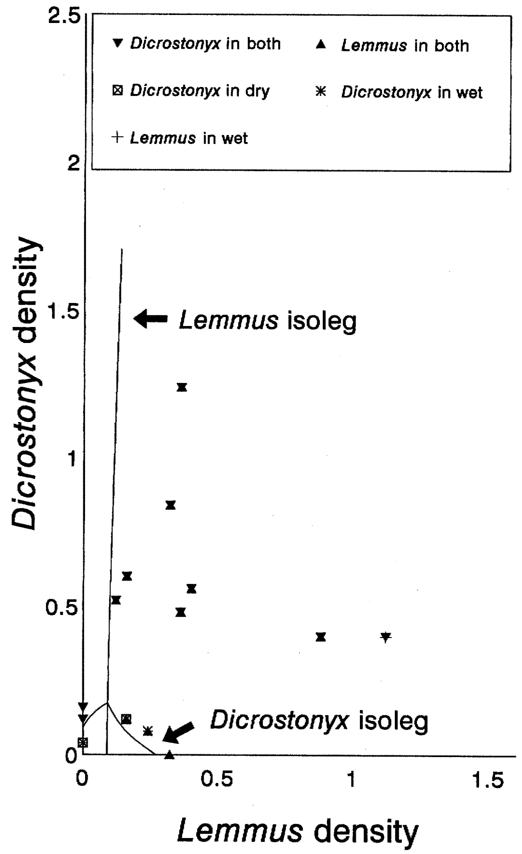

FIG. 3.—The absolute isolegs of *Dicrostonyx* and *Lemmus* in hummock and wet-meadow tundra habitats at Walker Bay in Canada's arctic. The near vertical line is the isoleg for *Lemmus*. The isoleg for *Dicrostonyx* has regions of positive and negative slope. The ghost region where each species occupies a separate habitat occurs in the irregular polygon in the lower-left corner of the graph (low densities of each species).

Competition with *Lemmus* creates a spectacular discontinuity in the collared lemming isoleg. To the right of the isoleg for *Lemmus*, brown lemmings occupy hummocks and reduce the density of *Dicrostonyx* in that habitat (the isoleg for *Dicrostonyx* has negative slope). To the left of the isoleg for *Lemmus*, brown lemmings occupy wet meadows only and the competitive effect in hummocks, representing a new kind of competitive ghost, disappears. But density of *Dicrostonyx* in hummocks also is reduced by the interaction between the two species in meadows. Thus, left of the isoleg for *Lemmus,* the isoleg for *Dicrostonyx* has a positive slope. The interaction terms, being multiplicative, create curvature in each species' isoleg (Fig. 3).

Data from 1997, when we captured only *Dicrostonyx,* appear to corroborate our interpretation. We recorded multiple captures of *Dicrostonyx* on two plots where they occupied both habitats. Both occur above the 1996 isoleg. We recorded single captures of *Dicrostonyx* on three other plots where both species were abundant in 1996. Two of the three captures were in hummock habitat, and both data points lie below the isoleg for *Dicrostonyx* in the ghost region. The third point is anomalous. The single collared lemming was captured in the wet meadow.

Lemming isoclines.—Although we need data when the species occur at intermediate densities, we probably know enough about each species' isoleg to infer their respective effects on competition. The zero-growth isoclines, for these species with fluctuating densities, occur only at respective minima and maxima of their population densities (Fig. 4). Other isoclines, positive when populations are growing, and negative during population decline, fill the state space.

Despite the negative effect on density of *Lemmus* in wet meadows caused by the interaction between lemming densities in wet habitat, the isocline for *Lemmus* is likely vertical throughout the state space (Fig. 4). The reason for this curious result rests with the standardized densities used to calculate the interaction terms (this transformation is necessary to remove autocorrelation between density and its interaction; e.g., Rodríguez, 1995). The value of the standardized interaction is high when the densities of both species in wet habitat is low, and it would also be high if both species were abundant in that habitat. But the data from Walker Bay show that when *Lemmus* is abundant in wet habitat, *Dicrostonyx* is not. Thus, the multiplicative negative effect from *Dicrostonyx* is spurious and reflects only the fact that when lemmings are sparse, density of *Lemmus* in wet meadows is necessarily lower than it is when lemmings are abundant.

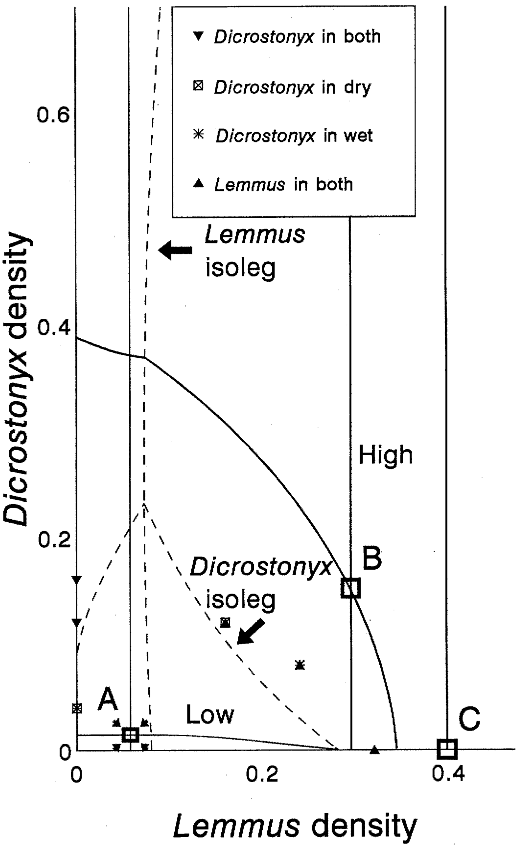

FIG. 4.—Absolute isolegs (dashed lines, from Fig. 3) and isoclines (solid lines) for two competing lemming species living in hummock and wet-meadow tundra habitats at Walker Bay in Canada's arctic. The isoclines for *Dicrostonyx* are either horizontal or negatively sloped; those for *Lemmus* are vertical. Three points of short-term "stability" (A, B, C) are indicated by bold squares and arrows. Isoclines correspond to low lemming densities (each species occupies a separate habitat—the ghost of competition, point A), and high densities where the species coexist in both habitats (point B, carrying capacity of *Lemmus* is less than the carrying capacity of *Dicrostonyx*) or where *Lemmus* exclude *Dicrostonyx* (point C, carrying capacity of *Lemmus* is similar to that of *Dicrostonyx*). There is no stable pair of zero-growth isoclines because the densities of both species vary through time.

The isocline for *Dicrostonyx* is far more interesting. Near the origin, where both species are at their respective low densities, each species occupies a separate habitat, and the isocline for *Dicrostonyx* is necessarily horizontal. At a somewhat higher density, *Dicrostonyx* occupies both habitats where it is affected adversely by the joint density of the two species in wet habitat. The interpretation of the interaction is vastly different from that for the isocline for *Lemmus.* Recall that the interaction is low when *Lemmus* is abundant in wet habitat, and note from the isodar that *Lemmus* is at least an equal, and perhaps a superior, competitor to *Dicrostonyx* in the hummocks preferred by collared lemmings (competition coefficient = 1.59). Thus, when *Lemmus* is abundant in wet meadows, it inhibits the use of wet habitat by *Dicrostonyx* and inflates density of *Dicrostonyx* in hummocks. The isocline for *Dicrostonyx* has negative slope. If one follows density of *Dicrostonyx* down its isocline, density of *Lemmus* in wet meadows increases, the interaction term is reduced, as is the competitive effect. In the zone where *Lemmus* occupies wet habitat only, the isocline for *Dicrostonyx* becomes slightly more shallow as density of *Lemmus* increases, and it is concave away from the origin.

If the density of *Dicrostonyx* is not too high, the isocline will cross the *Dicrostonyx* isoleg and become horizontal. If the density of *Dicrostonyx* is high, however, as it would be during a population peak, the isocline will cross the isoleg for *Lemmus* when *Dicrostonyx* occupies both habitats. *Dicrostonyx* will face increased competition from *Lemmus* that now inhabits hummocks, and the slope of the isocline for *Dicrostonyx* will become steeper. As the density of *Lemmus* increases further, a greater and greater proportion occupy hummocks, and the total competitive effect on *Dicrostonyx* will increase (the isocline is concave toward the origin;—Morris, 1999).

Whether ephemeral coexistence is possible at high densities will depend on the relative carrying capacities of each species. If the carrying capacity of *Dicrostonyx* is much greater than that of *Lemmus, Dicrostonyx* can overcome its competitive disadvantage with *Lemmus,* and isoclines will intersect in the zone where both species occupy both habitats (e.g., Fig. 4, point B). If, on the other hand, carrying capacity of *Lemmus* is equal to or greater than that of *Dicrostonyx, Lemmus* could capitalize on its competitive advantage and exclude *Dicrostonyx* from both habitats (e.g., Fig. 4, point C). Even so, the exclusion itself is likely to also be ephemeral as *Dicrostonyx* could reinvade hummock habitat from even drier areas where it maintains low-density populations. Carrying capacities will depend on the mix of habitats in the landscape, as will any patterns of coexistence.

DISCUSSION

I have tried to demonstrate how the study of habitat-dependent interactions can improve our understanding of distribution and abundance of similar species. In the case of voles and mice, we see that habitat selection can ameliorate effects of apparent competition. Indeed, habitat-selecting predators appear to create intersecting isoclines that enhance stable coexistence of two independent prey species. The perpendicular isolegs create a region where each species occupies a separate habitat, but it is not a ghost and has nothing to do with competition.

In the example from lemmings, habitat selection appears crucial for their competitive coexistence. Despite the potential for several points of stable competitive coexistence revealed by dramatically non-linear isolegs and isoclines for lemmings, the varying dynamics of lemmings guarantee that any apparently stable point is ephemeral. This does not mean that all zones of the state space contribute equally to the evolution of habitat-dependent coexistence of lemmings. Densities of lemmings fluctuate dramatically (Stenseth and Ims, 1993), and they are low enough to reside within the ghost region during relatively long intervals of time. Species can evolve adaptations to only those habitats to which they are exposed (Brown and Pavlovic, 1992; Holt and Gaines, 1992; Rosenzweig, 1987). Any prolonged period of ghostly densities will thus reinforce the habitat proclivities of each species.

One message from both studies is clear. To understand the coexistence of species, we must evaluate the role of habitat and habitat selection. But there also is a more fundamental message. Our new understanding about coexistence in these systems is based, through the habitat isodars, isolegs and isoclines, on evolutionarily stable strategies (ESS) of habitat use. The ESS approach reflects an exciting new paradigm where population dynamics and community organization emerge from the optimal behavior of individual organisms (e.g., Brown, 1996; Fryxell and Lundberg, 1997; Rosenzweig and Abramsky, 1997; Schmitz, 1997; Sutherland, 1996). Moreover, we see that habitat selection reveals the spectacular non-linearities that often arise through adaptive behaviors. Our ability to map those behaviors onto the dynamics of populations and communities may be the most lasting legacy that we have inherited from Robert MacArthur.

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