Habitat-dependent estimates of competitive interaction

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Regression analyses that use habitat and density data to estimate competitive interaction have a variety of limitations. Many of these shortcomings can be overcome by a modified analysis based on estimating habitat isodars; lines at every point of which the average fitness of individuals in one habitat is equal to that of individuals occupying other habitats. Isodars are part of a larger theory of spatial population dynamics that is independent of the classical Lotka-Volterra-Gause equations of density-dependent interspecific interactions. Isodar analysis simultaneously evaluates quantitative and qualitative differences between habitats as well as habitat-dependent species interactions. Isodar analysis can differentiate between exploitative and interference competition and can be used effectively in manipulative studies of species interaction. Analyses on two simple rodent communities implied density-dependent habitat selection but failed to find evidence of interspecific competition.

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Introduction

Habitat use depends upon both intra- and interspecific interactions. It should be possible to disentangle the effects of these two components on density-dependent habitat use. Early successes using multiple regression procedures to partial out intra- and interspecific effects on habitat use have been jeopardized by recent studies that identified a series of weaknesses in the regression analyses.

This paper presents an alternative method of density-dependent habitat analysis that should be capable of overcoming many of the limitations of the previous approaches. The method is promising because it also identifies qualitative and quantitative differences between habitats. The technique is capable of detecting asymmetrical species interactions as well as those that vary with habitat.

I begin by briefly describing the commonly used Schoener-Pimm regression technique and reviewing its limitations. I then discuss the theory of density-dependent habitat use for coexisting species to show another way it can be used to estimate species interactions from census data. I apply the model to real data and discuss its implications to the study of interspecific competition.

Regression estimates of interspecific competition

Theories of community organization depend primarily upon the magnitude and direction of interactions among species. The best estimates of these interactions come from careful manipulation experiments that usually involve the controlled removal of one or more species and subsequent monitoring of density compensation by supposed competitors. Under most field conditions this experimental protocol is very demanding of the investigator. The design and scope of the experiment may not be appropriate to the study organism's perception of time and space, and frequently the desired manipulation cannot be maintained with adequate replication for long periods of time. Even if the manipulation can be maintained, there is no guarantee that the experiment's spatial-temporal scale corresponds to that which should give a numerical response.

There are still other difficulties. The magnitude of the interaction itself may be density dependent and require

an array of density manipulations to reveal nonlinear responses. The interactions may have evolved under conditions of stable species coexistence with no current competitive effect (Schroder and Rosenzweig 1975, Rosenzweig 1979, Connell 1980) which means that a manipulation experiment may not even be capable of detecting the competition that is responsible for species' differences in habitat or resources.

The limitations of experimental methods for detecting and estimating competition prompted ecologists to develop simpler estimates of species interaction. Early work on niche theory suggested that the proportional overlap of limited resources could be used to estimate the intensity of competition (MacArthur and Levins 1967). The utility of these estimates are greatly restricted because the densities of interacting species may seldom be at equilibrium, resource dimensions are frequently interdependent, resource use often varies between populations, species and locations, and patterns of resource availability may have odd distributions that vary in space and time.

Attention has also focused on density-dependent competitive interactions which dictate the range and pattern of intra- and interspecific habitat use (Svärdson 1949, Morisita 1950 (cited in Rosenzweig, in press), Fretwell and Lucas 1970, Rosenzweig 1974, 1979, 1981, 1985, in press, Pimm and Rosenzweig 1981, Rosenzweig and Abramsky 1986). Schoener (1974) and Crowell and Pimm (1976) independently suggested that competition coefficients could be estimated by regression equations which evaluated density-dependent shifts in habitat use. Most tests have used Crowell and Pimm's (1976) protocol where the density of each species is regressed simultaneously against habitat structure and the density of supposed competitors. The technique has been used on simulated (Hallett and Pimm 1979) as well as real data (Dueser and Hallett 1980, Hallett 1982, Hallett et al. 1983, Rosenzweig et al. 1984, 1985, Abramsky et al. 1986) and has been criticized on theoretical grounds (Bender et al. 1984). Despite some success the assumptions of the analysis, as well as the published tests, suggest several problems with the method:

1) The analysis implicitly assumes that density-dependent competition occurs for microhabitats in short supply.

2) The analysis is incapable of determining the degree of density-dependent intraspecific habitat use unless all valid habitat predictors of density are included. Inclusion of uninformative habitat predictors likewise jeopardizes the analysis (Carnes and Slade 1988).

3) The analysis of intraspecific density-dependence will be biased whenever consumer density is not in equilibrium with resources.

4) The analysis of competitive interactions will be biased whenever competitor densities are not in equilibrium.

5) The linear analysis cannot compensate for non-linear competitive interactions. This is equivalent to stating that the competition coefficients are themselves density dependent. Schoener (1974, 1985) has discussed and used a variety of models to fit non-linear zero-growth isoclines.

6) The analysis applies only to the range of densities censused and to the range of values of the habitat variables.

7) The analysis may often be biased when collinear variables are included in the regression equation (Carnes and Slade 1988).

8) The analysis may be biased whenever comparisons are made between common and rare species (Rosenzweig et al. 1985, but see Pimm 1985).

9) The analysis will be biased whenever intraspecific density is a non-linear function of habitat. This problem can be at least partially overcome by curvilinear techniques (Rosenzweig et al. 1985) or by modified direct gradient analysis (Rosenzweig et al. 1984).

10) The analysis will be biased unless it simultaneously accounts for the density dependence of habitat use of all species that influence the density of other species in the community. This bias can be reduced by interspecific residuals analysis (Rosenzweig et al. 1984). Residuals analysis is unlikely to detect apparent competition (Holt 1977) and its relatives whereby the effects of omitted or uncensused species appear as erroneous interactions among the species actually included in the analysis.

11) The analysis will be biased whenever quantitative components of habitat do not positively covary with qualitative changes in habitat. Structural differences between habitat census sites need not be positively correlated with increased density because the sites themselves differ. These changes could be related to changes in productivity, to phenotypic changes between populations of consumers, or to the number and kind of interacting species. These effects can be assessed by scale analysis (Morris 1987a).

The difficulties of the Schoener-Pimm method, and the failure of niche overlap as a reliable indicator of competitive interaction, are discouraging to those of us who would like to be able to infer processes of community organization by looking at the patterns they create. Yet if our theories about density-dependent habitat selection and resource use are correct, we should be able to develop techniques based on census data to detect the paramount influences of density on patterns of distribution and relative abundance.

The spatial dynamics of competition

The theory of competitive interaction has concentrated on finding solutions to temporal dynamics of the Lotka-Volterra-Gause competition equations. Spatial dynamics are fundamentally different and are appropriately modeled in the context of density-dependent habitat selection theory. Density-dependent habitat selection of single species predicts that population density should
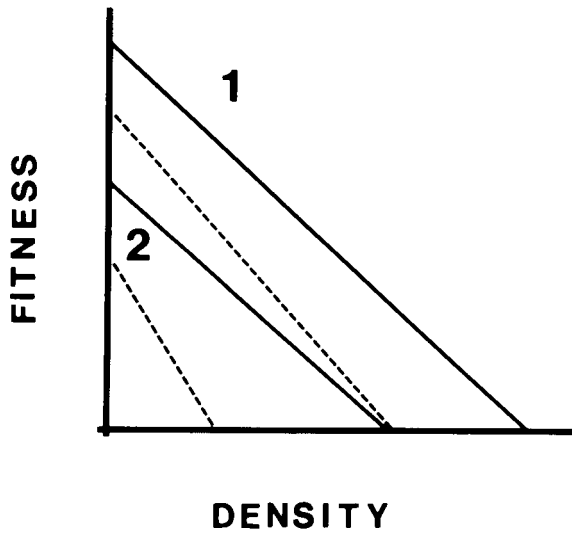
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DENSITY

Fig. 1. The Fretwell-Lucas theory of density-dependent habitat selection modified to show interspecific competition. Solid lines are the fitness-density curves of species A in habitats 1 and 2 in the absence of competition. Dashed lines represent one of an unlimited number of modifications of the fitness-density functions with interspecific competition. In this example the presence of a competitor has reduced both absolute fitness at low density as well as modifying the reduction of fitness with increased density.

reflect the expected fitness of individuals living in each habitat (Fretwell and Lucas 1970, Rosenzweig 1974, 1981). Habitats with higher resource renewal rates should support higher densities than habitats with lower resource renewal.

As population size increases, more demands are made on resources, and expected fitness should decline as a characteristic function of density (Fig. 1). The relative slopes and shapes of these curves among habitats will specify the spatial dynamics of the population as functions of reproductive success. Competitors, predators and other interacting species influence reproductive success, and consequently will influence the elevation, slope and/or shape of the fitness-density functions. If we could measure these effects we would have a fitness-related estimate of species interaction. These effects depend upon density, and we must simultaneously evaluate each species' use of habitat as a function of its own density and that of its competitors.

Morris (1987c, 1988) showed that intraspecific density-dependent habitat use could be evaluated by transforming fitness-density graphs to isodar plots. This is done by plotting the densities of species A in habitats 1 and 2 such that the expected fitness of individuals is identical in the two habitats (Fig. 2). If density in each habitat is adjusted such that average fitness in both habitats is more or less the same and decreases with increasing density, the analysis of replicated density estimates between the two habitats will correctly reveal the underlying pattern of density-dependent habitat use. The isodar for species A is given by

$$N_{A1} = C + b\,N_{A2} \tag{1}$$

where N_{A1} and N_{A2} are the densities of species A in habitats 1 and 2 respectively, C represents the quantitative difference between habitats and b is the isodar slope. A non-zero intercept indicates quantitatively different habitats, whereas isodar slopes different from 1.0 imply qualitative differences related to habitat-dependent population regulation and community structure (Morris 1987c, 1988).

Now assume a second species (B) also exploits both habitats and similarly is most abundant in habitat 1. Then its isodar will be

$$N_{B1} = C' + b'\,N_{B2}. \tag{2}$$

The equations follow Morris (1987c) who suggested that isodars be plotted as the habitat with the higher density against the habitat with the lower density. Species B could just as likely be most abundant in habitat 2, in which case the isodar would be

$$N_{B2} = C' + b'\,N_{B1} \tag{3}$$

and

$$N_{B1} = (N_{B2} - C')/b'. \tag{4}$$

If the two species compete exploitatively for habitat then the density of species A in habitat 1 will depend upon its density in habitat 2, the product of the density of species B in habitat 1 times its interaction with species A in that habitat, and the product of the density of species B in habitat 2 times its interaction with species A in habitat 2. For exploitative competition, the respective two-species isodars become
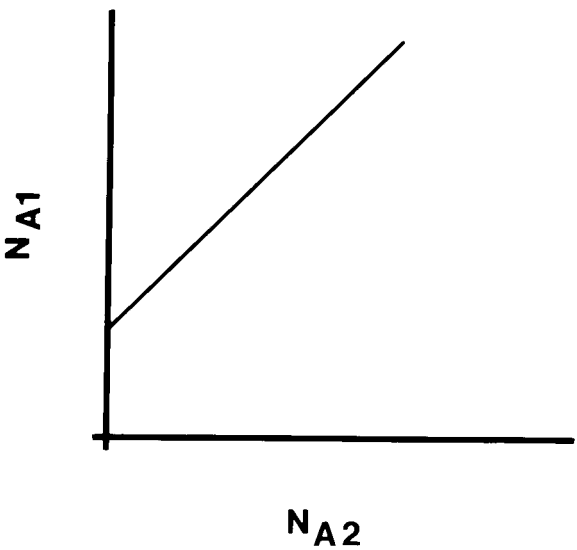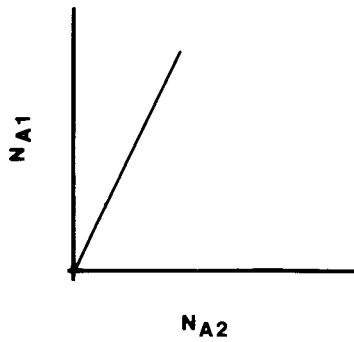

Fig. 2. An isodar graph of Fig. 1 (no competitive effect). Every point on the line (the isodar) reflects the densities (N_{A1} and N_{A2}) in habitats 1 and 2 where the average fitness of individuals of species A is identical in both. The curve is described by the isodar equation $N_{A1} = C + b\,N_{A2}$.
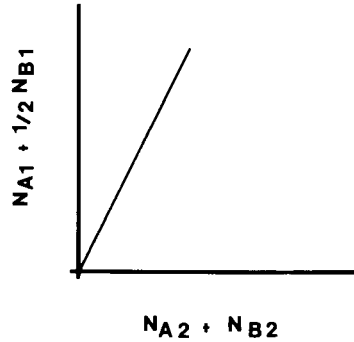
ALLOPATRY

SYMPATRY

Fig. 3. Isodars for the hypothetical example discussed in the text. The left diagram describes species A exploiting two habitats in allopatry ($N_{A1} = 2[N_{A2}]$). The right diagram shows species A exploiting both habitats in the presence of a competitor (species B) ($N_{A1} + 1/2[N_{B1}] = 2[N_{A2} + N_{B2}]$, rearranging, $N_{A1} = -1/2[N_{B1}] + 2[N_{A2}] + 2[N_{B2}]$). The slopes and intercepts of the isodars are identical.

$$N_{A1} + \alpha N_{B1} = C + b(N_{A2} + \beta N_{B2}) \qquad (5)$$

and

$$N_{B1} + \alpha' N_{A1} = C' + b'(N_{B2} + \beta' N_{A2}) \qquad (6)$$

where α is the competitive effect of one individual of species B on species A in habitat 1 and β is the same effect in habitat 2. α' and β' are the respective effects of species A on B in the two habitats. The intercepts of the single-species and two-species isodars are unchanged because we are evaluating the densities of the two species in each habitat as the equivalent of the density each species would have if it were the only occupant of the two habitats.

The rationale for the signs of the coefficients is as follows. If species A and B compete in habitat 1, the overall density of species A will be reduced by its competition for limited resources with species B. The density of species A will thus be reduced by B, and the equivalent density species A could achieve if B was absent is given by the sum of the two species corrected by the intensity of competition. In this way the slope of the two-species isodar is kept equivalent to that of the single species. Similar arguments hold for the sign of all coefficients.

What if the signs of the coefficients are different from those predicted by interspecific competition? A negative α implies some sort of reinforcing effect where the density of species A alone would be less than its density when it co-occurs with species B. Similarly, a negative β would imply reinforcement of the density of species A by species B in the second habitat. If species B has no effect on density-dependent habitat selection by species A, the coefficients would not differ from zero. The analysis would then be repeated on species 1 alone. Even though this paper deals with competition, other forms of interaction, as well as single-species density-dependent habitat selection, can be evaluated by the same regression techniques.

The utility of isodar theory in resolving species inter-

actions can be clarified by a hypothetical example. Imagine that allopatric and sympatric populations of species A and B occupy two habitats. For simplicity, assume that both habitats are equally productive (quantitatively identical) but that they are structurally different (qualitatively dissimilar). The structural differences between habitats mean that individuals of species A will be more efficient at extracting resources and converting them into descendants in habitat 1 than they are in habitat 2. For example, one individual of species A in habitat 2 could have the same depressive effect on the reproductive success of conspecifics as two individuals do in the more efficiently exploited habitat 1.

Using this example, consider first species A in allopatry. If A is a density-dependent habitat selector it should exist in habitat 1 at twice the density it has in habitat 2 because average fitness is identical in the two habitats only at this relative density. A habitat isodar is an empirical map of the set of densities where individuals have the same expected fitness in both habitats; in this case, the isodar will pass through the origin (no quantitative difference between habitats) and have a slope of 2.0 (reflecting the qualitative difference between the two habitats) (Fig. 3, left).

Now consider species A in sympatry with its competitor, species B. Assume that the average competitive effect of an individual of species B on species A in habitat 1 is one half the average effect of a conspecific individual. Equivalent exploitation of those resources available for species A in habitat 1 is achieved by its own density or double that density of individuals of species B. Equivalent exploitation could also occur among a large set of possible joint densities of species A and B between these extremes. The actual equilibrium at any one instant in time will depend in turn on the intensity of competition and on the joint densities of the two species in the second habitat.

To see this, assume that the competitive effect of individuals of species B on species A in habitat 2 is twice that in habitat 1 (interspecific and intraspecific effects

are equal). In allopatry, a density of 30 individuals of species A would be distributed as 20 individuals per unit area in habitat 1 and 10 individuals per unit area in habitat 2. In sympatry, the same degree of exploitation could occur over a range of density combinations (e.g., 18 individuals of A and 4 of B in habitat 1 and 5 individuals of each in habitat 2) (Fig. 3, right).

The crucial concept of this form of isodar analysis is that the degree of exploitation remains constant. If we know the competition coefficients we can plot the isodars in two-species space. The slopes and intercepts of the two-species isodars are equivalent to those expected for single species in allopatry (Fig. 3). This property allows us to calculate the coefficients empirically.

Rearranging (5) and (6),

$$N_{A1} = C - \alpha N_{B1} + b N_{A2} + \beta b N_{B2} \qquad (7)$$

and

$$N_{B1} = C' - \alpha' N_{A1} + b' N_{B2} + \beta' b' N_{A2} \qquad (8)$$

which can easily be estimated by multiple linear regression. Generalizing,

$$N_{A1} = C - \alpha \Sigma N_{n1} + b N_{A2} + \beta b \Sigma N_{n2} \qquad (9)$$

where summations are over n potentially competing species.

Equations (7) through (9) are suitable for the analysis of exploitation competition. Other kinds of competition may have different effects. It could be argued, for example, that interference should modify foraging efficiency causing qualitative differences between habitats. Since qualitative differences modify the slopes of isodars, the isodar slope may change as a function of the presence/absence of the competing species. This effect should be most pronounced for the subordinate species which suffers the most from interference competition. An appropriate two-species, two-habitat isodar equation including both exploitative and interference competition is given by

$$[N_{A1} + \alpha N_{B1} + \gamma(N_{A1} N_{B1})] =$$
$$[C + b \{N_{A2} + \beta N_{B2} + \varepsilon(N_{A2} N_{B2})\}] \qquad (10)$$

where γ and ε are scaling constants for the interference between species A and B in habitats 1 and 2 respectively.

Rearranging,

$$N_{A1} = C - \alpha N_{B1} - \gamma(N_{A1} N_{B1})$$
$$+ b N_{A2} + b \beta N_{B2} + b \varepsilon(N_{A2} N_{B2}). \qquad (11)$$

Interference competition has no effect on the isodar slope and intercept *as long as interference is included in the isodar equation*.

In practice, there are two major difficulties with Eq. (11). First, the interference of species A and B in habi-

tat 1 confounds an independent variable (the density of species B in habitat 1) with the dependent variable (density of species A in habitat 1). Second, the interference of species A and B in habitat 2 may result in multicollinearity among the independent variables. How can we overcome these problems? I can offer two alternatives. One, run the isodar regressions for each species including only the intraspecific densities and one of the interference terms. For example, the equation

$$N_{A1} = C - \alpha N_{B1} + b N_{A2} + b \beta N_{B2} + b \varepsilon(N_{A2} N_{B2}) \qquad (12)$$

can be used to estimate the importance of interference competition between A and B in habitat 2. Repeating the regression using N_{A2} as the dependent variable would estimate the importance of interference between the two species in habitat 1. Similar paired regressions for the second species would evaluate interference from the perspective of species B. A second solution would be to compare additive (exploitation) isodars before and after species removal experiments (or possibly between allopatric and sympatric populations). If the isodars were the same, we would have convincing evidence that interference was unimportant. If the additive isodars were different, we would conclude that the isodar was changed by some form of species-dependent interaction in addition to exploitation.

The isodar equations represent several improvements over most previous regression estimates of competition:

1) The competition coefficients are allowed to vary as a function of habitat.

2) The joint effects of density of all species on all other species' use of habitat is analyzed simultaneously (there is no need for a residuals analysis to estimate competition).

3) The isodar slopes detect qualitative differences between habitats, habitat-dependent differences in population regulation and the mode of community organization (Morris 1988).

4) The isodar intercepts indicate the degree of quantitative difference between habitats.

5) Interference competition can be evaluated through the inclusion of appropriate interaction terms.

6) The analysis is based on discrete habitat classifications and thus avoids complex interactions between the magnitude of habitat variables and population density.

7) The analysis requires only census data and habitat classification, not detailed habitat measurements. This has the additional desirable property of reducing the occurrence of collinear variables.

8) Carrying capacity is free to vary.

The model assumes that:

1) Species are in equilibrium with resource abundance (but not necessarily with one another).

2) Habitat selection is density dependent (verified if the regression equation is statistically significant).

3) Habitat selection is a linear function of density

(this can be evaluated by a plot of residual variation and can be corrected by curvilinear regression).

4) Competition coefficients are constant within any one specified habitat.

5) All species that influence density-dependent habitat selection by other species have been identified and unbiased estimates of their densities obtained simultaneously.

6) Qualitative and quantitative characteristics of the habitats are constant.

7) As in previous methods, the data meet the statistical assumptions of the analysis.

How would we interpret different alternative outcomes of the regression analysis for a two-species equation?

If, in an analysis of species A, all regression coefficients were statistically significant, we would conclude that species A is a density-dependent habitat selector which competed with species B in both habitats. This would suggest that the regression coefficients for species B would likely be significant also. The multiple regression equations would then be rearranged in the form of Eq. (5) and analyzed as isodars to evaluate quantitative and qualitative differences in habitat.

If, in an analysis of species A, only the regression coefficient for species A's density in the second habitat was statistically significant, we would conclude that species A is a density-dependent habitat selector which did not compete with species B. The correct isodar would then be determined by the model II regression of the density of species A in habitat 1 against its corresponding density in the second habitat (e.g. Morris 1988).

If, in an analysis of species A, one or more of the regression coefficients for species B were statistically significant but not the coefficient for species A in habitat 2, the analysis would suggest that species A's use of habitat is independent of density, but that species A competes with species B.

If, in an analysis of species A, at least one of the regression coefficients for species B was statistically significant as well as one or more of the interference coefficients, we would conclude that the two species compete exploitatively as well as interfering with one another. The dominant species should normally be the one with the higher interference coefficient. If we obtained the same result but none of the regression coefficients for species B were significant, then we would conclude that the two species were interference competitors only.

Lastly, if in an analysis of species A, none of the regression coefficients were statistically significant, we would conclude that species A is a non-competing species whose use of habitat is also independent of its own density. Analogous interpretations would hold for the analysis of any other species.

Isodar analyses on rodent species

It is difficult to find suitable data sets on which to apply multiple-species isodar analysis (MSI). I eventually settled on two for demonstration purposes only.

Morris (1983, 1984a, b, c, 1987a, b) studied the joint use of habitat patches by *Peromyscus leucopus* and *Microtus pennsylvanicus* in Point Pelee National Park on the northwest shore of Lake Erie. Small mammals were live-trapped in single plots located in two wooded (forest and sumac) and two open (grassland and old field) habitats. Each plot consisted of a 9×15 array of sampling points which were trapped at monthly intervals from May through October in each of 1978 and 1979. To obtain replicated density estimates in each habitat, I constructed five adjacent belt transects of 3×9 trap grids (Morris 1987b) and estimated density as the number of different individuals captured in each one per year. The methods and limitations of this census technique are outlined in Morris (1987b).

Microtus was common in the open habitats in both years, as was *Peromyscus* in the wooded habitats. *Peromyscus* occurred in the old field at low density in 1978 and at moderate density in 1979. *Microtus* was never captured in the sumac, and no more than four individuals were captured in the forest in any one year.

I previously performed three isodar analyses on *Peromyscus*, comparing forest and sumac, forest and field, and sumac and field habitats (Morris 1988). There was no reason to compare any given sub-plot with any other so I randomized the data and compared ten different combinations of densities. The analyses suggested congruent regulation (no qualitative differences, equal habitat preference) between the two wooded habitats, and divergent regulation (qualitative differences present) in comparisons of the woods and old field (*Peromyscus* 'preferred' the woods). It was possible that competition between *Microtus* and *Peromyscus* in the old field might have been responsible for the quantitative and qualitative differences I observed. At the time, I did not incorporate the possible *Microtus* effect into the isodar analysis, thus the first isodar regressions analyzed here looked for significant interference terms between species. These were not statistically significant and *Microtus* was effectively absent from the wooded habitats so the equations I evaluate below are

$$Pl(sumac) = constant + b_{s1} Pl(field) + b_{s2} Mp(field) \quad (13)$$

and

$$Pl(forest) = constant + b_{f1} Pl(field) + b_{f2} Mp(field) \quad (14)$$

where b_{si} and b_{fi} represent regression coefficients for the appropriate densities of *Peromyscus* and *Microtus* in the field for sumac and forest contrasts respectively. These analyses were conducted for the same random arrange-

Tab. 1. Representative MSI of *Peromyscus* density in the sumac against two predictors. *Peromyscus* macrohabitat selection was density dependent with no apparent competition with *Microtus*. Other randomizations of the input data yielded similar outcomes.

Source	df	SS	F
Pl(field)	1	576.44	34.68*
Mp(field)	1	5.82	0.35
Error	7	116.34	
Total	9	698.60	

* − p < 0.001

Tab. 3. MSI summary of *P. boylii* arboreal activity against three predictors. *P. boylii* microhabitat selection was density dependent with no apparent competitive interactions with *Neotoma*.

Source	df	SS	F
Pb(ground)	1	19.20	9.06*
Ns(arboreal)	1	0.92	0.43
Ns(ground)	1	7.06	3.33
Error	5	10.59	
Total	8	37.77	

* − p < 0.05

ments of the data as in the earlier single-species isodar analysis.

Holbrook (1979a, b) studied competitive interactions for ground and arboreal microhabitats by three cricetid rodents in Arizona. *Peromyscus boylii* and *Neotoma stephensi* were abundant, *P. maniculatus* was scarce. Rodents were live-trapped on grids, each of which consisted of 60 ground and 40 arboreal live-trap stations. Holbrook compared control with species removal plots to assess possible competitive interactions between species. *Neotoma* had a negligible effect on arboreal microhabitat use by *P. boylii*. Relative to controls, *Neotoma* marginally increased its use of arboreal habitat on the *P. boylii* removal grids.

I used Holbrook's control data (captures per microhabitat per grid per year, Tab. 2 of Holbrook 1979b) on *P. boylii* and *N. stephensi* to assess their competitive interaction by MSI. I did not include *P. maniculatus* because it was scarce, and because I used only nine replicated estimates of density. I first standardized the capture data assuming equal numbers of capture sites for ground versus arboreal traps, and further standardized these as the number of captures per 100 trapnights. These data best represent 'activity' rather than 'density'. The analysis is at the scale of microhabitat, and it seems appropriate to use activity data rather than absolute density estimates at this scale of analysis. Holbrook (1979b) also evaluated horizontal habitat use but I was unable to extract sufficient data to examine competition using that classification.

Preliminary isodar regressions including interference terms between species were not statistically significant so I evaluated the following additive equations.

$$\text{Pb(arboreal)} = \text{constant} - b_{a1} \text{Ns(arboreal)} + b_{a2} \text{Pb(ground)} + b_{a3} \text{Ns(ground)} \tag{15}$$

and

$$\text{Ns(ground)} = \text{constant} - b_{g1} \text{Pb(ground)} + b_{g2} \text{Ns(arboreal)} + b_{g3} \text{Pb(arboreal)}. \tag{16}$$

To evaluate the multiple-species isodars, both the Ontario and Arizona data sets were analyzed by multiple linear regression analysis (MINITAB) subject to the following protocol. For the dependent variable of species A in habitat 1, I entered the density of species A in habitat 2 as the first independent variable to evaluate intraspecific density-dependent habitat selection. I then entered the density of species B in habitat 1 followed by its density in habitat 2. These latter two independent variables were analyzed to evaluate whether or not either accounted for a significant proportion of the residual variation remaining after inclusion of intraspecific density-dependent effects. In all cases using the data I analyze here, I would have obtained exactly the same results had I used a stepwise entry procedure. I was unable to simultaneously assess competitive interfe-

Tab. 2. Representative MSI of *Peromyscus* density in the forest against two predictors. *Peromyscus* macrohabitat selection was density dependent with no apparent competition with *Microtus*. Other randomizations of the input data yielded similar outcomes.

Source	df	SS	F
Pl(field)	1	619.97	41.66*
Mp(field)	1	0.27	0.02
Error	7	104.16	
Total	9	724.40	

* − p < 0.001

Tab. 4. MSI summary of *Neotoma* ground activity against three predictors. *Neotoma* microhabitat selection was density dependent with no apparent competitive interactions with *P. boylii*.

Source	df	SS	F
Ns(arboreal)	1	3.88	23.95*
Pb(ground)	1	0.77	4.75
Pb(arboreal)	1	0.54	3.33
Error	5	0.81	
Total	8	6.00	

* − p < 0.005

rence because my sample sizes were too small to include additional independent variables.

All of the analyses revealed significant intraspecific density-dependent habitat selection (Tabs 1–4). None of the analyses produced significant interspecific competitive effects (Tabs 1–4).

The next stage in the analysis would normally use the intraspecific densities alone to calculate isodars of *P. leucopus* at Point Pelee and of *P. boylii* and *Neotoma* in Arizona. I have previously completed this analysis for *P. leucopus* and concluded that forest and sumac habitats were qualitatively and quantitatively superior to the old field (Morris 1988).

The model II regression estimates of the microhabitat isodars for *P. boylii* and *Neotoma* were

$$Pb(arboreal) = 1.73 + 1.26 \; Pb(ground) \tag{17}$$

and

$$Ns(ground) = -0.04 + 1.40 \; Ns(arboreal) \tag{18}$$

respectively. Neither of the intercepts were significantly different from zero, and the slopes were not significantly different from 1.0. These combined results suggest that the arboreal and ground stations were quantitatively and qualitatively similar for both species, and that competitive interactions had no significant effect on the use of either type of station.

Discussion

I have provided the isodar analyses of rodent habitat use primarily to demonstrate the utility of multiple-species isodar analysis (MSI) to problems of habitat use and competitive coexistence. Neither analysis should be interpreted as a definitive statement on habitat use by either rodent fauna. The results are still interesting. At the scale of macrohabitat (Point Pelee analysis), *P. leucopus* demonstrated density-dependent habitat selection. At the scale of microhabitat, both *P. boylii* and *N. stephensi* seemed to also show density-dependent habitat selection.

The Arizona results are ambiguous. Different stations used either a ground trap *or* an arboreal trap, not both. One simple explanation for the regression results is that different grids and years supported different numbers of the two rodent species. If these were captured at random over each study plot, we should expect a high correlation between their density in different sub-sets of the grid. This correlation need not imply anything about density-dependent habitat selection. This ambiguity would not have occurred if each station had been trapped with both an arboreal and a ground trap.

In the same context, it is not necessarily surprising that the two Arizona rodents showed equal preference for arboreal and ground traps. With one exception, the

distribution of arboreal and ground stations both corresponded to the distribution of 'horizontal' microhabitat types (Holbrook 1979a). As long as arboreal and ground traps have similar capture success for each species, the distribution of captures among arboreal and ground stations may simply represent random use of equivalent spatial microhabitats.

Holbrook (1979b) observed a microhabitat shift toward increased use of arboreal habitat by *Neotoma* when *P. boylii* was removed compared with when *P. boylii* was present. The direct estimate of competitive interaction using MSI did not find this pattern. Does this mean that MSI failed to capture the dynamics of competitive interaction in this system? Assuming that Holbrook's design was foolproof and that the magnitude of the microhabitat shift was ecologically 'significant', then strictly speaking, yes. On the other hand, MSI never had a fair chance. Regression estimates of competitive interaction cannot reasonably be extended beyond the range of densities in the analysis. Abramsky et al. (1986) made a similar point when invoking curvilinear species interactions to account for the failure of the Crowell-Pimm method to adequately predict competitive dynamics in bumblebee communities.

There are two important points to be made about the range of applicable densities of MSI. First, the possible curvilinear features of the interaction can be assessed when the entire range of densities is included in the analysis.

Second, if species normally do not experience the range of densities imposed by experimental manipulations, which interpretation of interaction are we to believe? I suggest that we place our confidence in the one that uses the natural dynamics of the system, rather than the one that manipulates it toward unusual densities. 'Press' (Bender et al. 1984) removal experiments only estimate the competitive effect when one or more species are absent. When we evaluate competition by species removal experiments, we implicitly assume the classical view that the interesting case of competitive coexistence corresponds to the conditions under which a rare competitor can invade an apparently stable configuration of species. This is only one view of the dynamics of competitive interaction. Competitive coexistence may instead be mediated at intermediate densities or exist in a non-equilibrium state maintained by immigration from allopatric populations (Maurer 1985, Schroder 1987). The more appropriate estimate of competitive interaction in this latter example is the one that is obtained from densities which correspond to those on the 'neutral ground' (Schroder 1987) of the sympatric zone. It is always interesting, nevertheless, to know the density-dependent effect of competitive interaction over the entire range of possible competitor densities to document domains of attraction for local stability. This is why I have suggested including MSI as part of the experimental protocol of competitive interaction. When this is impossible, I suggest that it is most practical to

know the density-dependent effect over the probable range of competitor densities.

A third point is short, but no less important. MSI provides a quick, and easy to use, method to evaluate quantitative and qualitative differences between habitats.

MSI implies that interacting species may frequently coexist at equilibrium with resource supply over a wide range of joint densities. The existence of these multiple combinations could account for much of the confusion over whether ecological communities frequently occur at equilibrium or not. Classical interpretations of competition theory have concentrated on evaluating equilibrium densities when populations cease to grow and after competition has been resolved. Isodar theory allows us to evaluate the dynamic equilibrium of coexistence during the process of competitive interaction. We can do this while population density changes in response to a variety of density-dependent interactions. Many of these interactions may prevent communities from achieving global or even local equilibrium in the classical sense; yet the structure of the community can still be the result of predictable density-dependent processes. One of the promises of isodar analysis is its ability to reveal not only these processes (e.g. quantitative and qualitative habitat differences) but also to reliably predict the kind, direction and intensity of interaction in apparently non-equilibrium settings.

The ambiguities of the Arizona analysis suggest that the greatest weakness of MSI may be its reliance on a priori habitat classifications. MSI implicitly assumes that the investigator's classification of patches corresponds to that of the study organisms. This apparent limitation of MSI is also perhaps its greatest strength. MSI demonstrates how species perceive the qualitative and quantitative patch structure of their environment. If the ecologist compares patches that the density-dependent habitat selector does not perceive as different, the analysis will produce slopes of unity and intercepts which are not significantly different from one another (equal preference, Morris 1988). This is what happened in my earlier analysis of *P. leucopus* in Point Pelee (Morris 1988). I initially suspected that a patch of three m tall sumac would support different densities of mice than a 20 m tall mixed forest. I was wrong. In the perception of *P. leucopus*, the two habitats were identical. Rather than being limited by my a priori perception of habitat use by *P. leucopus*, isodar analysis corrected it.

Future studies will, no doubt, more carefully identify the limits to isodar analysis. Isodar analysis is not perfect and MSI shares many of the logistical, theoretical and statistical limitations of other regression approaches that have been severely criticized by some ecologists (e.g. Rosenzweig et al. 1985, Abramsky et al. 1986). Bender et al. (1984) have suggested, for example, that regression estimates similar to MSI are defective because it is impossible to find natural sites where some

parameters vary and others do not (in MSI possible site differences in parameters would include α and species identity). I do not necessarily share this pessimism and have shown how some of these problems can be overcome by adding interaction effects to the isodar equations. Even if I completely agreed with Bender et al. (1984), I would not discard the technique; I would try to integrate it into the standard protocol of definitive density-dependent manipulations of competitive interaction. At the moment, MSI represents a reasonable alternative protocol to assess the magnitude and direction of habitat-dependent species interactions, and we can add to the list above, the following improvements over previous techniques:

9) MSI demonstrates the qualitative and quantitative perceptions that organisms have of their habitats.

10) By analyzing habitat use at different spatial scales, MSI should be able to infer the spatial scale of density-dependent habitat selection as well as the scale at which habitat selection is influenced by species interactions.

11) As long as the assumptions of the analysis are met, MSI is capable of predicting population density in alternative habitats as a function of both habitat and community organization.

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