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Habitat-dependent competition and the coexistence of Australian heathland rodents

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When competing species depress one another's fitness in the habitats that they occupy, their competitive effects will emerge in each species' pattern of density-dependent habitat choice. Thus, a regression analysis of joint densities, corrected by the habitat effect, should reveal the magnitude of interspecific competition. We tested this idea by 1) demonstrating the connection between removal experiments and regression estimates of competition with those obtained from isodars (regressions that implicitly incorporate evolutionarily stable strategies of habitat selection) and 2) evaluating whether interspecific competition inferred from isodars corresponded with the inferences emerging from regression and field experiments. Previous removal experiments on two herbivorous rodents occupying coastal wet heathlands in eastern Australia documented that competition between *Rattus lutreolus* and *Pseudomys gracilicaudatus* is asymmetrically biased in favor of the much larger *Rattus*. The asymmetry in competition was also revealed by regression estimates of competition. Isodar analyses illustrate a habitat-dependent mechanism for the asymmetry. *Rattus* compete effectively with *Pseudomys* in both 'wetter' and 'drier' patches of heath whereas *Pseudomys* appear to exert a competitive effect in only the drier sites. The magnitude of competition measured by a removal experiment in an area with more-or-less equal amounts of both habitats will be biased in favor of *Rattus*. More generally, one can use the isodar estimates to draw isolegs and isoclines of competitive coexistence. Isoclines for the two Australian rodents imply dynamic equilibria of stable competitive coexistence that vary with plant succession in fire-dominated heathland ecosystems.

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Estimates of species' interactions are crucial to any analysis of the rules structuring ecological communities. Reliable estimates can be obtained from carefully controlled and replicated field experiments (e.g., Abramsky et al. 1991, 1994, Higgs and Fox 1993, Thompson and Fox 1993). If species interactions act to structure communities, they must influence spatial-temporal patterns of abundance. With appropriate care, we should be able to reconstruct the interactions from patterns of species abundance as long as we know the processes that create those patterns.

Interspecific competition will frequently be mediated via processes of density-dependent habitat selection (Svärdson 1949, Fretwell and Lucas 1970, Rosenzweig 1974, 1979, 1981, 1991, Pimm and Rosenzweig 1981, Pimm et al. 1985, Morris 1988, 1989, 1999a, b). Indeed, many kinds of community structure explicitly invoke interspecific density-dependent preferences for habitat

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(Pimm and Rosenzweig 1981, Rosenzweig 1981, 1989, 1991, Rosenzweig and Abramsky 1986, Morris 1988). Not surprisingly, a variety of methods exist by which one can use habitat-dependent patterns of density to measure interspecific competitive effects.

When species compete for habitat, the average competitive effect corresponds to the weighted difference between the density attained in each habitat in the absence of the competitor(s). The effect can be measured by field experiments that remove or manipulate the density of each species (e.g., Abramsky et al. 1991, 1994, Higgs and Fox 1993, Thompson and Fox 1993 as recent examples for mammals, and many others [Connell 1983, Schoener 1983, Dueser et al. 1989]). A parallel approach compares habitats where pairs of competitors coexist, with similar habitats where each species exists alone (Schoener 1974).

One may also control the habitat effect statistically by the use of regression (Crowell and Pimm 1976, Hallett and Pimm 1979) if the habitat and competitive influences are represented by standardized partial regression coefficients (Fox and Luo 1996, Luo et al. 1998). The habitat effect is usually encapsulated in a series of variables expected to correlate with animal abundance. Any mis-specification in the regression model (e.g., an inappropriate or incomplete set of habitat variables, unaccounted curvilinear or nonlinear relations of density with those variables) can bias the estimate of competition.

Morris (1989) developed an alternative based on habitat isodars (Morris 1987, 1988) that represent evolutionarily stable strategies of habitat selection (e.g., Fretwell and Lucas 1970, Pulliam 1988, Pulliam and Danielson 1991, Morris 1994). A habitat isodar is the plot of densities in two or more habitats such that the expected fitness of an individual is the same in each (no individual can improve its fitness by moving to another habitat). The isodar will depend on the densities of any species that cause a density-dependent reduction in fitness of the focal species.

The central theme of habitat in techniques to estimate competition suggests a common theoretical basis that should allow us to translate from one technique to the others. We begin the translation by demonstrating the correspondence between isodars and removal experiments and by demonstrating how the regression method emerges from isodar theories of competitive coexistence. We do not do the same with the Abramsky/Rosenzweig method because isodars are implicit in its application (e.g., Abramsky et al. 1991). We illustrate our solution by comparing isodars with the results of controlled field experiments, and with regression estimates of interspecific competition, between a pair of coexisting murid rodents in eastern Australia.

Theories of habitat selection and estimates of competition

Imagine a pair of species with distinct preferences for two different habitats (Fig. 1: at low density species 1 prefers habitat *A*, species 2 prefers habitat *B*). Imagine, as well, that for each species the fitness an individual can expect to achieve in each habitat declines with increased population density. An evolutionarily stable strategy of habitat selection emerges when the expected fitness is the same in both habitats (ideal habitat selection). For illustrative purposes, imagine that species 1 occupies both of its habitats, and that species 2 occupies its preferred habitat only (low density). Species 2 should depress the expected fitness of species 1 in habitat *B* (Fig. 1). If the expected fitness of species 1 remains constant in both habitats, its density in habitat *B*, as well as its overall density, will be reduced (Fig. 1). A comparable argument will cause a parallel effect of competition by a small number of individuals of species 1 on species 2. The competitive effect is revealed in the isodars,

$$N_{1A} = c + bN_{1B} + b\beta N_{2B} - \alpha N_{2A} \qquad (1)$$

and

$$N_{2B} = c' + b'N_{2A} + b'\beta' N_{1A} - \alpha' N_{1B} \qquad (2)$$

where N_{ij} equals the density of species i in habitat j, c is the isodar intercept, b is its slope, and α and β represent habitat-dependent competition coefficients (Morris 1989, 1999a, b, Fig. 1, bottom, assumes additive effects only, multiplicative effects can be incorporated easily by transformations and interaction terms [Morris 1989, 1992, 1994]).

Note that the value of the competition coefficient obtained in a removal experiment will depend on the magnitude of the habitat-dependent competition coefficients weighted by the densities of the competitor in the two habitats. For species 1,

$$\alpha^*_{12} = (\alpha N_{2A} + \beta N_{2B})/(N_{2A} + N_{2B})$$

where α^*_{12} represents the average competitive effect of species 2 on species 1. The removal experiment is redundant with the isodar estimate of competition.

How is the Crowell-Pimm regression method of estimating interspecific competition linked to isodars? Imagine, as above, that species 1 and 2 compete for a pair of habitats but that each has a distinct habitat preference, and that values of ‘microhabitat’ variables differ between habitats. Imagine first that the competitor is absent, but that the density of the focal species varies. Imagine, as well, that the number of occupied sites in a habitat is proportional to population density. The ratio of the focal species’ densities in the two habitats, representing its habitat preference, declines with population size ($N_{1A}/N_{1B} = [c + bN_{1B}]/N_{1B}$; Fig. 1). The mean value of microhabitat, calculated as the average of the values of microhabitat at occupied sites, also varies with population size. The regression coefficient of microhabitat on population density will be significant.

Now let the competitor vary in density. Increased density of the competitor reduces fitness of the focal species within habitats where the competitor occurs. The isodar intercept of the focal species is greater than in the absence of the competitor, the ratio of densities in the two habitats at any population size is more biased toward the preferred habitat ($N_{1A}/N_{1B} = [c + bN_{1B} + b\beta N_{2B}]/N_{1B}$), as is the mean value of microhabitat (assuming, again, that the number of occupied sites is proportional to population density and, in this example, that the competitor occupies habitat *B* only). The difference in habitat selectivity that occurs with differential numbers of competitors represents the competitive effect. Residual variation about the regression of population density on microhabitat will be accounted for by the density of the competing species.

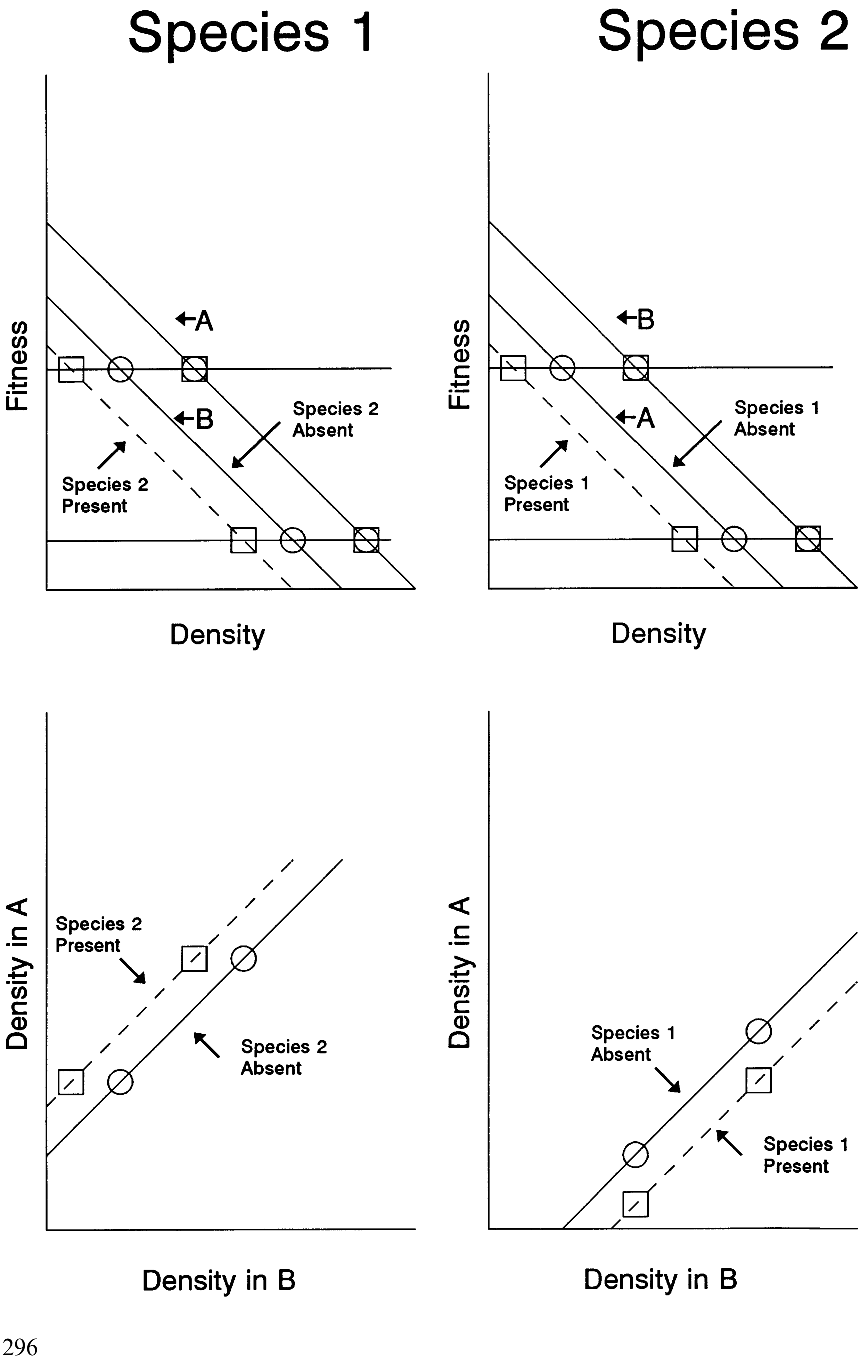

Fig. 1. Examples of the relationships between fitness and density for two species with distinct habitat preferences for two different habitats (*A* and *B*). Top. The fitness and corresponding density of each species in the two habitats when it occurs alone (solid lines) compared with the expectation when it occurs in the presence of a small number of its competitor (dashed line, the competitor has reduced the fitness in the habitat it occupies). Bottom. The isodar in the absence of the competitor (solid line) is different from the isodar where the competitor is present (dashed line). The competitor has, in each case, reduced the mean density, and increased the selectivity, of the focal species. Symbols represent ideal-free densities in the presence (squares) and absence (circles) of the competing species. Other kinds of ideal distributions can be modeled similarly (Morris 1988, 1994, 1999a).

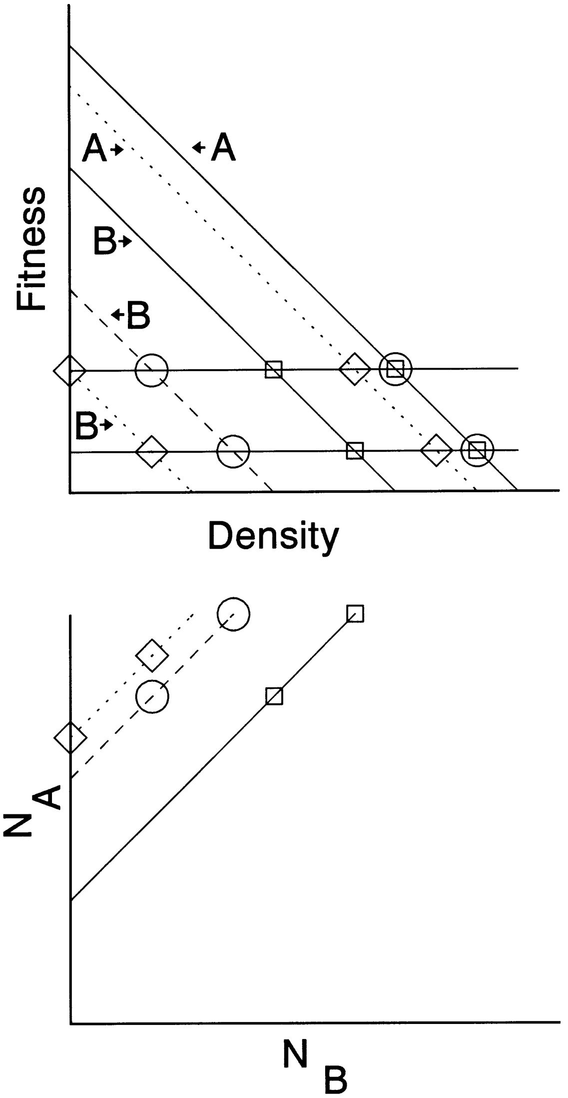

Fig. 2. An example of the habitat-dependent competitive effect for two habitats when one is co-occupied by two competing species. Top. Fitness-density curves of species 1. Solid lines – species 1 alone, dashed line – species 2 (the competitor) is present in its preferred habitat (*B*) only, dotted lines – species 2 occupies both habitats. Symbols represent the evolutionarily stable strategy of ideal-free density-dependent habitat selection by species 1 (squares – species 2 is absent, circles – species 2 is present in habitat *B* only, diamonds – species 2 is present in both habitats). Parallel solutions apply to any form of ideal habitat selection. Bottom. The isodar intercept, and thus, the ratio of densities in the two habitats at any given population size, increases with increasing density of the competitor.

As the density of the competitor increases, it too will attain an equal expectation of fitness in each habitat and should occupy both. Even though the competitor will reduce fitness of the focal species in both habitats, the effect will be greatest in the focal species' secondary habitat (Fig. 2). Habitat selectivity of the focal species will continue to increase with increased density of the competitor. Thus, we see that habitat use depends on both intra- and interspecific densities, and the regression estimate of competition emerges from the isodar. Reversing the argument, one could subdivide a microhabitat gradient into two habitat types. The isodar estimate of competition would then emerge from the regression method.

The similarity between isodars and the Crowell-Pimm procedure would seem to depend not only on the assumption that microhabitat use is proportional to density, but also on habitat heterogeneity. If habitat patches fall easily into two types, as they might if the patches are large and merge along a single boundary, both techniques should be dominated by the major habitat differences and are likely to yield similar estimates of competition. If the habitats occur as a mixture of small patches, however, differential biases may emerge from the census assumption that individuals occurring in a given patch are actually exploiting the habitat when they are recorded there. Fine-grained foragers must pass through a variety of patches whether they exploit the resources in those patches or not. A typical census will simply record presence/absence in each patch, not whether individuals are actually exploiting them. Biased estimates of competition may emerge if species differ in their susceptibility to observation/capture in different patches or if they differ in the grain size at which they exploit the environment (this could occur through differences in mobility, differences in perception, or even through differences in habitat specialization). The problem is likely to be most severe when the scale of analysis is itself 'fine grained'. Estimates of abundance in a single area reflect only local processes and may distort our assessment of competition. Isodars integrate densities across patches, they implicitly increase the scales of both the census and its analysis, and should reduce the bias.

The comparison of techniques, and indeed our ability to estimate competition, may become clouded when patches vary in size. Individuals optimizing their exploitation of fine-grained patches should equalize the expected marginal benefits obtained from foraging in each patch (e.g., Brown 1988). At the larger coarse-grained scale, individuals choosing to live in one habitat over another are likely to equalize their long-term fitness (e.g., Morris 1992). A study that mixes fine and coarse-grained scales may inadvertently test two different measures of fitness, and two different mechanisms of habitat choice. A comparison of studies conducted at different scales will encounter the same problem. But any differences in density related to scale are likely to be minor in comparison to the dominant signal caused by differences in competitive ability between species. Isodars should reveal the competitive interaction.

Other complications arise when both habitats are occupied by both species (Morris 1999a). The depression in fitness in each habitat would depend simultaneously on the densities of the two species in each of their preferred and secondary habitats. Several alternative combinations of densities may be possible as the two species co-adjust their habitat preferences. The problem will become more acute if population size changes during the adjustment period. On the negative side, dynamic preferences and the specter of multiple states dash hopes we might have for predicting abundance in a given habitat (N_{ij}). On the positive side, however, multiple states emphasize the strength of the isodar approach because they have no influence on our ability to estimate competition. Any change in density of one species in either habitat must necessarily involve compensating changes in the density of the other. Even though the densities vary, the competition coefficients in eqs 1 and 2 are constant, and can thus be estimated by regression.

Habitat selection and competition between two Australian rodent herbivores

Rattus lutreolus (swamp rat) and *Pseudomys gracilicaudatus* (eastern chestnut mouse) co-occur in coastal wet heathlands in eastern Australia (Fox 1982, Higgs and Fox 1993, Thompson and Fox 1993). The coexistence is dynamic with the smaller *Pseudomys* occupying recently burned sites, then being gradually replaced by *Rattus* (Fox 1982, 1990, 1996). Removal of *Rattus* from experimental plots resulted in increased density of *Pseudomys* (Higgs and Fox 1993, Fox and Luo 1996). Compared to controls, *Pseudomys* on removal plots shifted their spatial preference toward sampling stations previously occupied by *Rattus* (Higgs and Fox 1993). While swamp rats appear to be the superior competitors, the relative degree of superiority is tied to habitat, particularly with respect to different successional stages. Differential habitat selection appears to also account for asymmetric competition between *Rattus lutreolus* and *Pseudomys higginsi* (Monamy and Fox 1999).

The habitat effect was confirmed by Fox and Luo (1996). The density of each species was associated with measures of habitat structure, but with a significant residual effect related to the density of the competing species. *Rattus* was revealed as a superior competitor to *Pseudomys*, a result that has also been demonstrated by experiment (Higgs and Fox 1993, Thompson and Fox 1993). The competition coefficient varied with the age of the heath (Fox and Luo 1996), confirming earlier speculation that competition between the two rodent species varies as the heath vegetation changes through time (Fox 1982).

The competitive effect of *Pseudomys* on *Rattus* also varies seasonally. Removal of *Pseudomys* from wet heath in summer resulted in a higher rate of increase of *Rattus* density in removal plots than in controls. Rising water levels caused rats to move out of even wetter swamp habitats and into wet heath (Thompson and Fox 1993). The difference in population growth rate was asymmetrically biased toward small swamp rats that preferentially immigrated into the experimental plots where similar-sized *Pseudomys* had been removed. Large *Rattus* appear immune to competition from *Pseudomys*. Similar removals during winter yielded no appreciable response from the *Rattus* population that has few small individuals at that time of year (Thompson and Fox 1993).

Methods

We accumulated data on the relative abundances of *R. lutreolus* and *P. gracilicaudatus* from intermittent rodent censuses in a single patch of wet heath conducted over a period of eight years (1989–1996). Each census included two three-night trapping periods conducted simultaneously in four separate 12-station trapping grids (20 m trap spacing). At times, our grids served as controls for species-removal experiments (Thompson and Fox 1993). Census data were collected during the non-removal period only.

We classified each station on each grid using two-way indicator species analysis (TWINSPAN, Hill 1979) on the percentage cover of each plant species measured at every trapping station during 1996 (Curran 1996). The analysis was used to generate the two habitats required for isodar analyses of rodent competition. We confirmed the habitat designations before beginning isodar analyses by ground-truthing each station during March 1997. We reclassified a station only if we could be certain that the relative abundance of indicator species near the station was biased because they were present in one of the original systematically oriented sample quadrats (four 1 m × 1 m plots at each trap station), but were not represented in the same way for the remaining area surrounding the station.

We estimated the relative density of each rodent species as the number of individuals captured standardized to the number of stations belonging to each habitat on each grid (number of individuals expected if the entire plot consisted of a single habitat type). We selected the subset of data where each species co-occurred in both habitats for the isodar analysis.

Using each species' density in each habitat as the dependent variable, we searched four possible isodar equations (Table 1) for significant density-dependent competitive effects by stepwise multiple linear regression (probability to enter $= 0.1$, probability to remove $= 0.15$; Norušis 1992). This rather atypical approach is necessary because each regression estimates different habitat-dependent competition coefficients (Table 1).

Rodríguez (1995) suggested a simpler alternative where one first calculates the isodar coefficients by standard minor axis regression (e.g., McArdle 1988), then rearranges the equation to produce each separate isodar. This approach is valid when species compete for identical resources in similar ways so that the basic quality of each habitat is independent of species identity. The per capita effect of each species on basic quality in each habitat is constant, and one can obtain any isodar equation from any other. Thus, if species 1's isodar equation is

$$N_{1A} = c + bN_{1B} + b\beta N_{2B} - \alpha N_{2A},$$

then for species 2,

$$N_{2B} = b^{-1}\beta^{-1}(-c + \alpha N_{2A} + N_{1A} - bN_{1B}).$$

For many competing species, however, habitat quality is likely to be far more idiosyncratic because species differ in the kinds of resources that they use, in their methods of resource harvest and conversion into descendants, in their susceptibility to predation and other risks, and in the 'rules of thumb' that they may use with respect to fitness and habitat selection. A simple hypothetical example may help to make this point clear. Imagine two competing species occupying two habitats, and consuming the same resource in each. Imagine, as well, that $b = 1$, $\alpha = 0.25$, and that $\alpha_{12B} = 0.5$, where α_{12B} is the exploitative effect of species 2 on species 1 in habitat B. Imagine, further, that species 1 only is susceptible to predation risk in habitat B, and that its behavioral response to the risk of predation (ϕ) reduces its ability to harvest resources [$\phi = f(N_{1B})$]. The actual competitive effect of species 2 in habitat B is thereby equal to its exploitative effect (α_{12B}) that reduces the density of species 1 in habitat B, plus its indirect effect through a behaviorally mediated reduction in the rate of density-dependent resource harvest by species 1. The isodar coefficient will be different from the pure exploitative effect. But, since species 2 is not itself differentially susceptible to the predation risk, its isodar slope ($b^{-1}\beta^{-1}\alpha$) is proportional to the exploitative effects only. Similar arguments could be made about other kinds of differences between species and between habitats. It seems reasonable to assume, as we do here, that isodars need to be solved separately within each habitat (Table 1).

Table 1. Four isodar equations necessary to evaluate competitive interactions between two species occupying two habitats.

$$N_{1A}=c+bN_{1B}+b\beta N_{2B}-\alpha N_{2A}-\gamma(N_{1A}N_{2A})+b\delta(N_{1B}N_{2B})$$

$$N_{2A}=C+BN_{2B}+B\varepsilon N_{1B}-\zeta N_{1A}-\eta(N_{1A}N_{2A})+B\xi(N_{1B}N_{2B})$$

$$N_{1B}=c'+b'N_{1A}+b'\beta'N_{2A}-\alpha'N_{2B}-\gamma'(N_{1B}N_{2B})+b'\delta'(N_{1A}N_{2A})$$

$$N_{2B}=C'+B'N_{2A}+B'\varepsilon'N_{1\mathrm{A}}-\zeta'N_{1B}-\eta'(N_{1B}N_{2B})+B'\xi'(N_{1A}N_{2A})$$

We completed the isodar analysis by calculating partial regression coefficients for the reduced regression models using the standard minor axis method of McArdle (1988, Rodríguez 1995). We chose not to follow the traditional bootstrap approach because our estimates of animal density should represent a habitat-dependent bias rather than a truly random sample of the possible range of rodent densities in wet heath.

We analyzed the data for both untransformed and logarithmically transformed data to determine the possible role of interference competition in *Rattus* and *Pseudomys* coexistence (Table 1, Morris 1992, 1994). The densities (or ln transformed densities) of each species were centered and standardized before calculating interaction terms (Montgomery and Peck 1982, Rodríguez 1995) that should be significant predictors of density when species interfere with one another (Morris 1989). Note that this procedure removes the mean densities from the interaction terms that have high values when the densities of both species are high or low.

Our samples represented two successional intervals since fire (22–27 months, 60–99 months) where rodent succession (Fox 1982) could complicate our attempts to measure competitive interactions between *Rattus* and *Pseudomys*. We controlled for this effect by first analyzing data combined from both intervals followed by a second analysis of the second period when *Rattus* were well-established on our grids.

We used the same data in a parallel analysis to assess the regression method for categorical habitat variables. We created a single binary indicator variable representing wetter and drier habitats. Using the density of each species as the dependent variable in two stepwise multiple regressions, we assessed whether the inclusion of habitat identity would allow us to properly interpret competitive interactions between the two rodent species.

We supplemented our tests of competition with census data collected from four similar 12-station grids in a second isolated patch of heath burned by wildfire in October 1994. Rodent censuses corresponded to three three-night trap sessions at roughly two-week intervals separated by periods of three to five months (heath succession from 3 to 20 months post-fire). Stations within each grid were classified via TWINSPAN on floristic data collected during 1996 (Monamy 1998). We accumulated the number of captures by species for each trapping interval in each habitat and analyzed for significant interactions between habitat, species' relative density, and the time of each census. A significant three-way interaction would confirm the role of habitat in determining the spatial-temporal distributions of the two rodent species. The number of independent estimates of rodent density were insufficient for a second isodar analysis.

Table 2. Summary of significant isodar regressions (ln transformed densities) between swamp rats and chestnut mice occupying wetter and drier habitats within wet heathland in eastern Australia. All coefficients are statistically significant ($P < 0.05$).

Regression equation	Source	Df	F	P
ln *Rattus N* (drier) = 3.22 -0.96^1 ln *Pseudomys N* (drier)	Regression Error	1 16	5.56	0.032
ln *Pseudomys N* (drier) = 3.02 -0.76 ln *Rattus N* (drier) $+0.62$ interaction (wetter)^2	Regression Error	2 15	5.62	0.015
ln *Pseudomys N* (wetter) = 2.91 $+0.3$ ln *Pseudomys N* (drier) -0.73 ln *Rattus N* (wetter) $+0.71$ interaction (wetter)^2	Regression Error	3 14	8.77	0.0016

[1] partial regression coefficients (model II); [2] product of centered and standardized ln transformed densities of each species in wetter habitat.

Results

TWINSPAN readily distinguished between 'wetter' and 'drier' habitats within the wet heath (Curran 1996). Wetter sites were characterized by species with well-known preferences for wet habitats (e.g., *Gymnoschoenus sphaerocephalus*, *Leptospermum juniperinum*). Drier sites were identified by species such as *Mitrasacme polymorpha*, and *Epacris microphylla* as well as species typically associated with dry heath (e.g., *Banksia aemula*, *Kunzea capitata*). The wetter-drier designation was confirmed by significant differences in soil moisture (Curran 1996). Eleven of the 96 stations appeared to have biased vegetation samples relative to the abundance of the indicator species and were reclassified accordingly. The number of stations in each habitat was essentially equal (49 drier, 47 wetter, the proportion of stations belonging to the drier habitat on any given grid varied between 0.25 to 0.75).

Rattus lutreolus and *Pseudomys gracilicaudatus* coexisted in both wetter and drier habitats in 26 of the 61 samples where at least one species was present. Each grid was represented in the final set of 26 samples at least once. Swamp rats were twice as abundant as chestnut mice (mean *Rattus* density in 'wet' = 8.4 compared to 5.0 for *Pseudomys*, mean *Rattus* density in 'dry' = 8.8 compared to 3.9 for *Pseudomys*).

None of the regressions using all 26 samples was statistically significant. Three of the four isodar regressions using data only from the second sample period (60–99 months) were significant (Table 2). Logarithmically transformed data provided, in each case, a marginally higher coefficient of variation and a better fit of predicted to observed values (Table 3).

The marginal, but consistently improved, fit of the logarithmically transformed isodars over arithmetic data supports the argument that competition between *Rattus* and *Pseudomys* is mediated by interference (Higgs and Fox 1993). Changes in population density caused by competitors appear to represent multiplicative effects rather than linear ones. The differences between the two analyses were not dramatically different, however, and the level of interference of *Rattus* on *Pseudomys* in the wild will need to be measured by experiment.

The density of *Rattus* in the drier habitat was influenced negatively by the density of *Pseudomys* ($\alpha_{RPd} = -0.96$, where subscripts denote species and habitats respectively, P = *Pseudomys*, R = *Rattus*). The situation was different for *Pseudomys* whose density in both habitats was reduced by *Rattus* ($\alpha_{PRd} = -0.76$; $\alpha_{PRw} = -0.73$, Table 2). Thus, given that the two habitats were represented evenly in our sample, the competitive effect of *Rattus* on *Pseudomys* is about twice that of *Pseudomys* on *Rattus*. Competition is asymmetrically biased against chestnut mice because they are inferior competitors to swamp rats in both habitats.

Despite the significant isodar equations, substantial variation in *Rattus* density was unexplained by the regression. We interpret the residual variation to reflect an apparent absence of density-dependent habitat preferences in wet heath during the period when *Rattus* was abundant (Fig. 3). The situation was dramatically different for *Pseudomys*. Chestnut mouse density in the wetter sites was clearly correlated with density in drier areas, but only when the regression included the overriding competitive dominance of *Rattus* (Fig. 3).

The second regression analysis using an indicator variable to represent habitat also revealed competition between the two rodent species (Table 4). The partial regression coefficients with competitor density were similar for both highly significant equations, suggesting that competitive interactions for habitat are similar for both species. The regression for *Pseudomys*, however, also included habitat identity. Thus, *Pseudomys* is negatively affected by the density of *Rattus*, and is marginally less abundant in the drier of the two habitats. The regression failed to capture the experimentally demonstrated asymmetry in competition, but did hint at a significant role for habitat in understanding the joint dynamics of swamp rats and chestnut mice.

Habitat-mediated effects on competition were also apparent in the separate analysis of habitat differences in capture rates of the two species following fire. Captures of each species varied with time, but the pattern varied between wetter and drier habitats (species × time × habitat interaction, L.R. $\chi^2_4 = 31.88$, $P < 0.0001$). *Pseudomys*, that had no habitat preference shortly after fire, switched to a preference for the wetter habitat as the number of *Rattus* captures increased with time (Fig. 4).

The significant interactions in the wetter habitat in our isodar analyses help us understand the time-dependent competitive effects in habitat preference. In the isodar analyses, the density of chestnut mice was less than it otherwise would be (the standardized interaction was negative) when one or the other species was rare in the wetter habitat while the second was abundant. The interaction effect has potentially important consequences to the way we view rodent succession following fire. *Rattus* is very abundant, while *Pseudomys* is rare, during the relatively late stages of succession (Fox 1996). At these times, the isodars suggest that *Rattus* overflows its preferred wetter habitat and depresses the density of *Pseudomys* in both habitats. *Pseudomys* is abundant, while *Rattus* is rare, during early stages of succession, and *Pseudomys* occupies both habitats. The time-dependent difference in relative abundance, and the dynamic changes in vegetation density of each habitat, probably account for our inability to detect competition when we mixed early and later stages of succession in our isodar analysis. The density of *Pseudomys* is, nevertheless, less during early succession than it is during the intermediate stages. *Pseudomys*' density declines again in late succession leading, eventually, to local extinction if the area remains unburned for a sufficiently long time (Fox 1996).

Discussion

The asymmetrical competitive dominance of *Rattus lutreolus* over *Pseudomys gracilicaudatus* revealed by removal experiments and regression estimates of competition was also confirmed by the isodar analyses. The asymmetry appears to have a strong habitat component whereby *Rattus* and *Pseudomys* compete strongly in drier sites within jointly occupied wet-heath habitat. Within the wetter sites, however, *Rattus* reduces the density of chestnut mice with no reciprocal effect. Regardless which habitats are represented in an experimental plot, the removal of *Rattus* will reduce its competition with *Pseudomys*. Conversely, the effect of removing *Pseudomys* will depend critically on habitat composition. The removal experiment should have greater effect in areas dominated by drier sites than in areas that are composed of wetter habitat. Whenever the two habitats are represented, the competitive effect of *Rattus* will always exceed that of *Pseudomys*.

The alternative regression technique using a habitat indicator also implicated habitat-mediated competition between the two rodent species, but it failed to document the strong asymmetry in competitive ability between them. It thus appears that regression methods, if they are to be used to estimate the magnitude of competition, need to incorporate quantitative information on habitat 'quality' (e.g., Fox and Luo 1996). This conclusion emphasizes our earlier point that the Crowell-Pimm method is linked to density-dependent changes in habitat preferences with increased population density.

If *Rattus* is the superior competitor, why did chestnut mice on the recently burned site switch toward the wetter habitat where they have little competitive effect on *Rattus*? Could the answer lie in isodar theory? The isodar coefficient for the intraspecific effect corresponds to the ratio of slopes of the fitness-density functions in each habitat (Morris 1988). A slope greater than one implies that habitat preferences diverge with increasing density, but a slope less than unity implies convergence with the possibility that habitat preferences switch with increased density. The best habitat at low density is not the best at high density. Switched habitat preferences can probably occur by a variety of mechanisms. Habitat preferences may switch, for example, if predation risk is both habitat and density dependent. Predation in habitat *A* may be low at low prey density because

Table 3. Comparison of the predictive value of isodar equations using untransformed vs logarithmically transformed rodent densities.

Equation	Dependent variable	R^2* and significant variables	
		Untransformed density	Transformed density
1	*Rattus* N in wet	0 (no sig. variables)	0 (no sig. variables)
2	*Rattus* N in dry	0.20 (*Pseudomys* N in dry)	0.21 (ln *Pseudomys* N in dry)
3	*Pseudomys* N in wet	0.35 (*Rattus* N in wet, *Pseudomys* N in dry)	0.58 (ln *Rattus* N in wet, ln *Pseudomys* N in dry, interaction in wet)
4	*Pseudomys* N in dry	0.34 (*Rattus* N in dry, *Pseudomys* N in wet)	0.35 (ln *Rattus* N in dry, interaction in wet)

* Adjusted R^2.

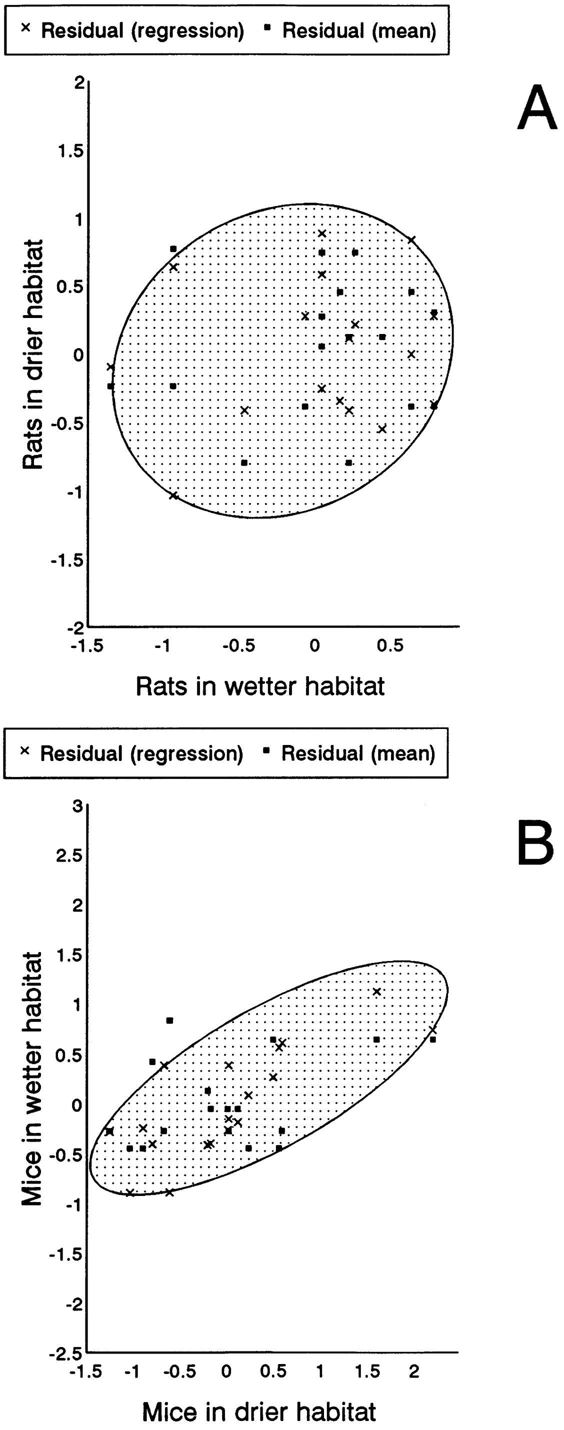

Fig. 3. Partial regression plots demonstrating the ability of isodars (ellipses) to explain the habitat-dependent densities of *Rattus lutreolus* (A) and *Pseudomys gracilicaudatus* (B) occupying wetter and drier trapping stations in wet heathlands in coastal New South Wales. ■ – standardized residual densities from the mean density of each rodent species in each habitat (no competition), × – standardized residuals from the significant isodars of each species (competition).

predators are rare (numerical response) or foraging elsewhere (a form of functional response). The nature of either response could reverse habitat quality for prey when they are abundant.

It is more likely that the intraspecific coefficient in *Pseudomys'* isodar reflects a combination of time-dependent habitat preference as well as the habitat-mediated competitive effect from *Rattus*. Early in succession, neither habitat is dense enough to meet the requirements of *Rattus*. Both habitats, however, are dense enough at this stage to be occupied by *Pseudomys* (Higgs and Fox 1993). The temporal and successional link is invisible to the isodar, except as a distorted image of density. The results of our isodar analysis illustrate that *Pseudomys* appears to prefer the wetter habitat at low density, and to gradually shift its preference to the drier, where it can compete successfully with small *Rattus*, as density increases. But the habitat preferences are dynamic and depend on the density of vegetation, as well as the pattern and speed of habitat recovery following fire (e.g., Fig. 4).

Time-dependent competition

Experiments confirm our interpretation that *Pseudomys'* habitat use reflects complexities of temporal changes in habitat and associated habitat preferences following fire. Treatments that removed most of the ground-level vegetation documented a clear threshold of vegetation density below which both *Pseudomys* and *Rattus* discontinued their use of manipulated sites (Monamy 1998). On treatments that removed less vegetation, *Rattus* discontinued its use of the treatment sites but *Pseudomys* was unaffected (Fox B. J., Taylor J. E. and Thompson P. T. unpubl.). The two experiments demonstrate that the threshold for *Rattus* lies above that for *Pseudomys*. The experiments also suggest that our designation of wetter and drier sites represent surrogates of habitat preference along which competitive interactions mold the local pattern of rodent coexistence. Vegetation cover in each habitat type varies among heathlands and with time since fire. The preference of wetter versus drier habitats exhibited by *Pseudomys*, and its competition with *Rattus*, will thus depend on the amount and variance of vegetation density in the two habitat types.

Early in succession both species are likely to prefer the wetter sites that 'recover' from fire most quickly. Increased density of *Rattus* during succession will displace *Pseudomys* from the most dense sites. The displacement will not affect *Pseudomys'* preference for the wetter habitat if the majority of drier sites are unavailable because they lie below *Pseudomys'* preference threshold. Increased density of *Rattus* will produce the opposite apparent preference by *Pseudomys* for drier habitat when most of the wetter sites are above *Rattus*' threshold while most of the drier sites are between the respective thresholds of both species. In intermediate stages of succession, drier sites become more dense and more suitable for *Rattus* that displace *Pseudomys* to the least dense, drier sites. Late in succession, shading causes the ground layer to open up in the wetter sites that now become more suitable for *Pseudomys* than the still dense drier ones. If the area remains unburned for a long enough period of time, the ground layer becomes less dense in both habitats that will again be temporarily suitable for *Pseudomys*, and unsuitable for *Rattus*. Habitat preference for *Pseudomys* swings back and forth between wetter and drier sites during succession. Both habitats can eventually become unacceptable for *Pseudomys* if the interval between fires is very prolonged.

The process of succession itself depends on local and environmental conditions. *Rattus* is absent from heathland rodent communities until habitat has recovered sufficiently to provide adequate cover for foraging and runway construction, and usually becomes abundant only after several years following fire (Fox 1982, 1990, 1996). On the recently burned site, however, *Rattus* populations were well-established within seven months since fire. The early invasion by *Rattus* appeared to be cued by rapid vegetation recovery on this particular site that receives substantial runoff from adjacent heathlands (Monamy 1998). The disparate responses of the two species to time since fire, compared with consistent responses to vegetation density, suggest that rodent 'succession' relates more to vegetation density than to time per se (Monamy and Fox in press).

Catling (1986) also reported an example of early recolonization of burned heath by *Rattus lutreolus*. The absence of *Pseudomys* from Catling's study site sug-

Table 4. Summary of significant regressions (ln transformed densities) between swamp rat and chestnut mouse density when they jointly occupy wetter and drier habitats within wet heathland in eastern Australia (habitat included as a binary indicator variable). All coefficients were statistically significant ($P<0.05$ unless otherwise noted).

Regression equation	Source	Df	*F*	*P*
ln *Rattus* $N = 3.04$ -0.63[1] ln *Pseudomys* N $+0.46$ interaction[2] (R^2 adj $= 0.37$)	Regression Error	2 33	9.88	0.0004
ln *Pseudomys* $N = 2.64$ -0.50 ln *Rattus* N $+0.31$ interaction -0.24 habitat[3] (R^2 adj $= 0.38$)	Regression Error	3 32	8.25	0.0003

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[1] partial regression coefficients (model I); [2] product of centered and standardized ln transformed densities of each species; [3] scored 0 and 1 for wetter and drier habitats respectively, $t = -1.8$, $P = 0.079$.

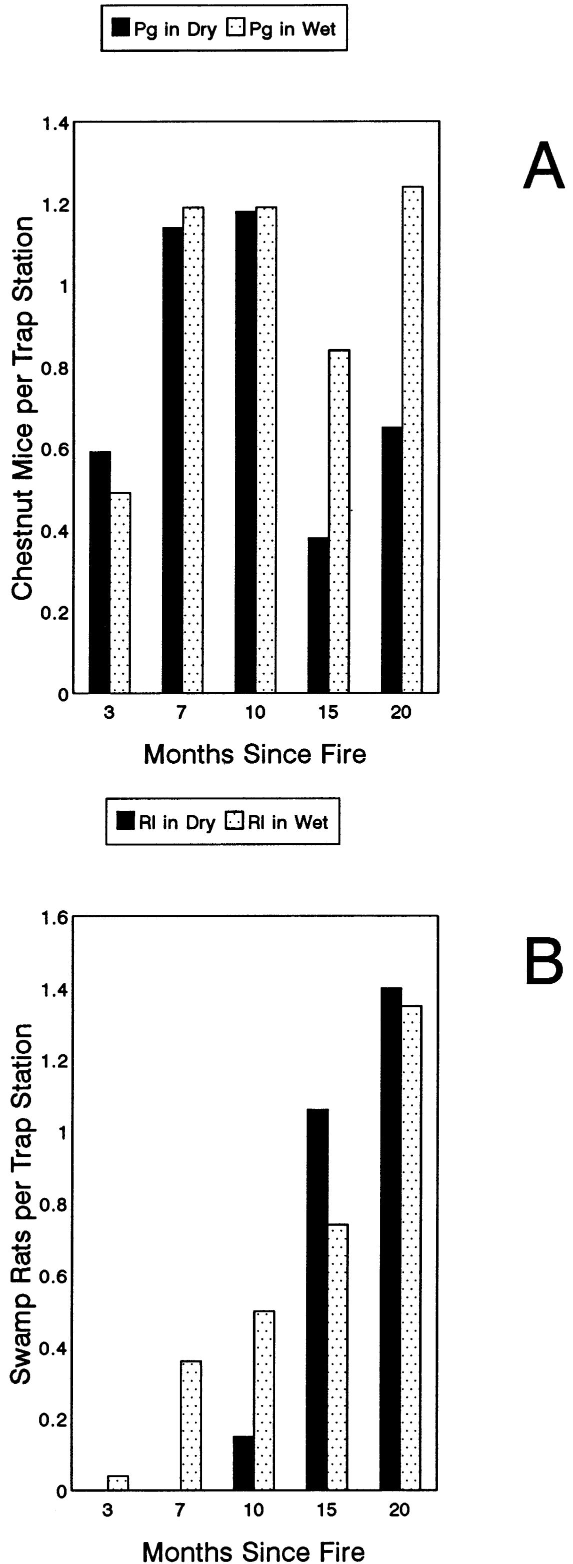

Fig. 4. Captures of *Pseudomys gracilicaudatus* and *Rattus lutreolus* in wetter and drier wet-heath habitats following fire. *Rattus* initially prefers wetter habitats but loses its habitat preference with time. *Pseudomys* has no initial preference but switches to the wetter habitat as the density of *Rattus* increases.

gested that early recolonization by *Rattus* might represent competitive release from *Pseudomys* (Catling 1986). Our data on the recently burned site refute the competitive-release hypothesis because *Rattus* increased shortly after fire in the presence of *Pseudomys* (Monamy 1998). The hypothesis is also rejected because every study to date has yielded consistently low estimates of *Pseudomys*' competition on *Rattus*.

Isolegs and isoclines

The *Rattus* and *Pseudomys* isodars, by identifying the degree of intra- and interspecific competition for habitat, allow us to draw each species' isoleg and associated isocline (Morris 1999a, b, Morris et al. 2000). Isolegs, corresponding to boundaries of habitat choice (Rosenzweig 1974, 1979, 1981, 1991), allow one to identify areas in the state space of species densities where habitat overlap, and associated per capita competition, is high and low. Once we know the pattern in per capita competition we can draw caricatures of the respective isoclines and infer the stability of species coexistence (Abramsky et al. 1991, 1994).

We begin by noting that *Rattus* density in the drier sites was reduced as the density of *Pseudomys* in drier habitat increased. High *Pseudomys* density in the drier habitat also implies high overall *Pseudomys* numbers (Fig. 3). *Rattus*' preference for wetter habitats (*Rattus*' isoleg) must increase with *Pseudomys* density. But recall that *Rattus*' habitat preference was independent of its own density in wet heath. The *Rattus* isolegs, corresponding to ever increasing preference for the wetter habitat, are horizontal (Fig. 5). The absence of habitat preference in wet heath does not mean that *Rattus* is incapable of density-dependent habitat selection. *Rattus*' habitat preference is clearly defined at a larger scale where it is replaced by its congener, *Rattus fuscipes*, in dry heathlands (Fox 1996).

The situation for *Pseudomys* is also interesting because both of *Pseudomys'* isodars include approximately the same level of competition from *Rattus* (Table 2). Increasing density of *Rattus* alone has no effect on habitat choice by *Pseudomys*. *Pseudomys*' preference toward the wetter habitat declined as its density increased in the drier habitat (isodar slope < 1). *Pseudomys*' isolegs must also be horizontal (Fig. 5), but opposite those for *Rattus*, they correspond to increasing preference toward the drier habitat. If this was the only competitive effect, interspecific competition would be lowest at high *Pseudomys* density. The significant interaction term in each isodar, however, demonstrated that *Pseudomys* density in each habitat was reduced when one species was abundant in the wetter habitat while the other was rare. The end result is that per capita competition is highest when *Pseudomys* is rare while *Rattus* is abundant, lowest when both species are abundant (they tend to occupy different habitats), and intermediate when *Rattus* is rare while *Pseudomys* is abundant (Fig. 5).

We used Fig. 5 to infer the general shapes of the rodents' isoclines (Fig. 6). High per capita competition on *Pseudomys* in the northwest and southeast quadrants, and low competition when both species are moderately abundant, produces a dramatically non-linear *Pseudomys* isocline (Fig. 6). For *Rattus*, per capita competition is most intense when *Pseudomys* is rare (arrow in Fig. 5), and its isocline is concave away from the origin. The two isoclines cross at a point of stable coexistence because interspecific competition coefficients in our isodars were less than one, the value of intraspecific competition in the same habitat (Morris et al. 2000). The point of intersection is biased toward *Rattus* because it is the superior competitor.

It is important to note, however, that our data correspond to only relatively late stages of pyric succession in wet heathlands. Other isoclines will apply during

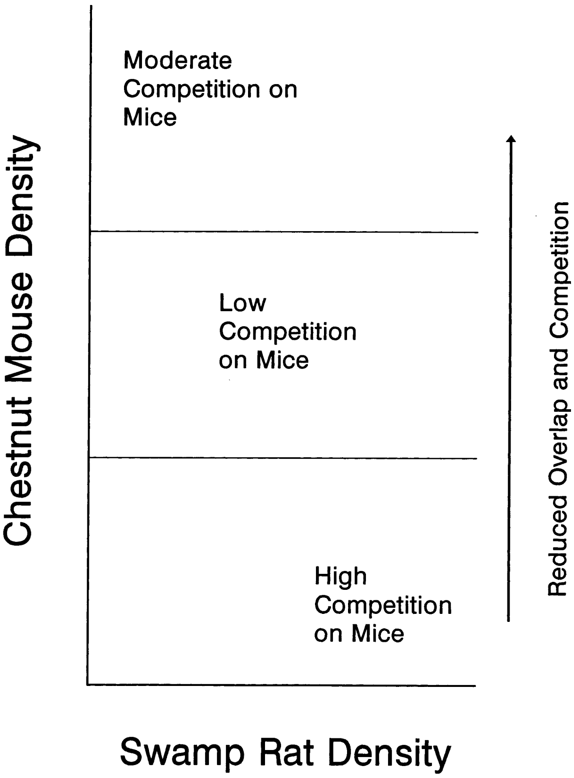

Fig. 5. Horizontal isolegs of *Rattus* and *Pseudomys* occupying wetter and drier trapping stations in wet heathlands lead to reduced habitat overlap and reduced per capita competition as the density of *Pseudomys* increases (arrow). Per capita competition on *Pseudomys* is relatively high in the northwest and southeast quadrants because interactive effects reduce the density of *Pseudomys* when one or the other species is abundant in the wetter habitat. Competition on *Pseudomys* is low when both species exist at moderate densities (the interaction is near zero).

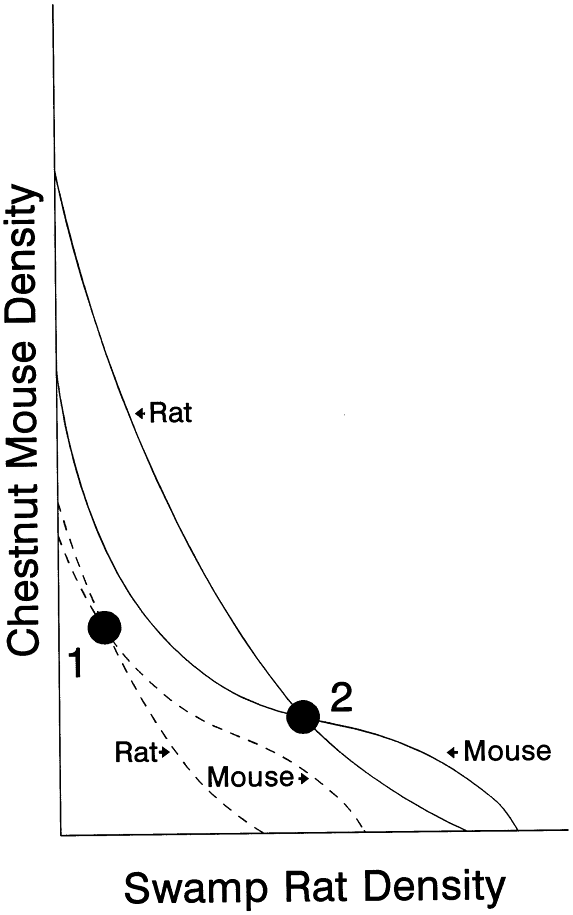

Fig. 6. Caricatures of the zero-growth isoclines for co-occurring *Pseudomys gracilicaudatus* and *Rattus lutreolus* during late and earlier pyric succession in wet heathlands in eastern New South Wales. Points of equilibria are indicated by filled circles and numbers. *Rattus* dominate during late succession (point 2). The dashed isoclines represent one possibility of what might happen during earlier stages of succession when *Pseudomys* is the most abundant species (point 1).

earlier stages of succession. We illustrate one example using patterns of density-dependent competition similar to those that we have described here (Fig. 6). The main point, however, is that different isoclines, and their ephemeral equilibria, will apply throughout succession.

Regardless, our results indicate that census estimates of competitive interaction often yield reliable estimates of interspecific competition. We are encouraged that isodars, with their emphasis on adjacent habitats, not only demonstrate the asymmetry observed in field experiments, but that they also implicate time-dependent habitat selection as a prime mechanism influencing the competitive coexistence of swamp rats and eastern chestnut mice. We are also encouraged that the habitat effect was readily apparent even though the boundary between the wetter and drier habitats was more or less arbitrarily defined, and even though habitat preferences varied through time. If theories of habitat selection can be used to properly interpret nonlinear competitive interactions between rodents in continuously varying wet heathlands, they will likely work even better at disentangling competitive interactions in systems where habitat boundaries are more clearly defined.

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