



Research article

Shadows of predation: habitat-selecting consumers eclipse competition between coexisting prey

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Abstract. Ecologists have made substantial progress evaluating the influences of adaptive behaviors on population dynamics and communities. But no-one has examined the joint influences of stochastic variation, predators, and density-dependent habitat selection on our interpretations of species coexistence. I begin the search with simulation models of habitat isodars (lines along which the fitness of individuals is identical in two or more habitats) assuming ideal-free habitat selection by two prey species exploited by a habitat-selecting parasitoid ‘predator’. The models include both regulating and non-regulating stochasticity. The intriguing results include the following: (1) all three species often achieved a true ideal-free distribution; (2) predators reduced prey population sizes and increased the frequency of local habitat extinctions; (3) despite the predator’s differential reduction of prey densities, there was no evidence of apparent competition; (4) all species exhibited pulses of dispersal associated with donor–receiver population dynamics; (5) isodars produced valid estimates of competition between prey only in constant environments lacking habitat-selecting predators; (6) habitat-selection by predators forced prey into their preferred habitats; (7) the resulting ghost of competition obscured the prey species’ competitive interaction; (8) isodars correctly revealed density-dependent habitat selection by the predator. Overall, the results appeared to depend primarily on the predator’s habitat choice, rather than on prey trade-offs between competitive ability and reduced value (handling time) to the predator. Habitat selection theory, and its revelation via isodars, can thus provide considerable insight into processes affecting real communities, and most especially if ecologists assess carefully the constraints for their analysis and interpretation. Nevertheless, isodars designed to measure competition are likely to be most reliable in donor-controlled or experimental systems where regulating stochasticity has relatively little influence on prey dynamics.

Key words: coexistence, competition, density-dependence, dispersal, habitat selection, host–parasitoid interactions, isodar, population dynamics, predation, sources and sinks, stochasticity

Introduction

Despite 50 years of progress and synthesis, ecologists continue to debate issues of population regulation (e.g., Turchin, 1999, 2001), the role of competition in the coexistence of species (Abrams, 2001), and whether we can measure

competitive interactions in the field (e.g., Morris *et al.*, 2000a, b). The road to consensus is obstructed by intricate and often interdependent dynamics of ecological systems. Even simple communities composed of a handful of species possess an amazing array of possible patterns of coexistence (Abrams, 1993; Holt *et al.*, 1994; Brown, 1996). The dynamics of coexisting species are made more perplexing by time lags, and non-linear and stochastic effects (May, 1973; Turchin and Taylor, 1992). Spatial variability in population regulation (Kareiva, 1990; Tilman and Kareiva, 1997), in dispersal (Huffaker, 1958), and in extinction and colonization probabilities (Levins, 1969; Hanski, 1999), create added complexity. Numerous possible community structures add to the confusion as they emerge from variation in environmental grain, and in the spatial scale of habitat use (Brown and Pavlovic, 1992). Resolution of the debate is made more difficult because competing species interact via a suite of bewildering mechanisms of coexistence (e.g., Kotler and Brown, 1999), while at the same time qualitative and quantitative differences among habitats yield a rich diversity of alternative community organizations (Pimm and Rosenzweig, 1981; Rosenzweig and Abramsky, 1986; Morris, 1988).

Yet if you challenge experienced field biologists to find a particular species, most will know where and when to look for it. They will know what kind of community is likely to exist in a particular area, they will know which species are abundant, and which ones are sparse, and they will have a general understanding of fluxes in abundance and distribution. Whether these patterns reflect the entire suite of possibilities revealed in model communities, and an uncanny ability by skilled naturalists to sieve pattern from noise, or whether they represent a subset of possibilities, is a moot point. Populations and communities possess detectable, and presumably repeatable, patterns.

It would be foolish to imagine that the patterns reflect equilibria amongst species whose populations fluctuate in time and space. Rather, individuals may interact with one another in quite consistent ways, and, because species differ from one another, so too do their interactions. Regardless whether the joint dynamics of species approach equilibria or chaos, consistent interactions amongst individuals should lead to consonant patterns if we know where to look for them.

One promising possibility is that interactions within and among species can be revealed by the ways in which they use and share habitat. Qualitative and quantitative differences in habitat yield dramatically different types of community organization (Rosenzweig, 1974, 1981, 1991; Pimm and Rosenzweig, 1981; Morris, 1988; Brown and Pavlovic, 1992). Experiments manipulating joint abundance in adjacent habitats reveal non-linear competitive interactions among species (Abramsky *et al.*, 1990, 1991, 1992, 1994), that can be measured by multiple regression along habitat isodars (Morris, 1989, 1999a; Rodríguez, 1995; Morris *et al.*, 2000a, b). The basic argument is that habitat use reflects

competitive and other interactions among species, regardless whether the constituent populations can, or do, exist at dynamic equilibrium.

Current theories of habitat selection are, nevertheless, based on classic models of populations and the dynamics of competing species within a single trophic level in constant environments (e.g., Morris, 1999b, 2000, 2003a; Morris *et al.*, 2000a, b, 2001; see Brown, 1998 for an alternative that models habitat selection under the risk of predation). Yet we have known for a long time that numerical responses by shared predators can cause the dynamics of otherwise non-competing prey to appear as though the prey species are actual competitors (apparent competition, Holt, 1977, 1984). Many other 'apparent' interactions among prey can also be driven by shared predation, and most especially so in heterogeneous environments composed of two or more habitats (Holt, 1984). Indeed, there is compelling evidence that spatial heterogeneity is essential to maintain coexistence of predators and parasitoids with their prey species (Huffaker, 1958; Beddington *et al.*, 1978; Holt, 1984; Kareiva, 1990; Holyoak, 2000). Habitat selection by predators, for example, can enhance prey coexistence because predators choosing among spatially-segregated prey are likely to be absent from patches with insufficient prey numbers to support viable predator populations (Holt, 1984). Though many predators are likely to partition habitats at somewhat different scales than their prey, there is abundant documentation of prey species that respond behaviorally to habitat differences in predation (e.g., Kotler, 1984; Kotler *et al.*, 1993; Morris, 1997; Brown *et al.*, 1999; Grand and Dill, 1999; Morris and Davidson, 2000).

It is thus of rather considerable interest to evaluate prey coexistence when both the prey and their predators are capable of habitat selection at the same spatial scale (as might occur along the borders of any pair of habitats where predators can exercise habitat choice). I explore the consequences of joint habitat selection by predators and coexisting prey by simulation. Many, if not all, species exist in stochastic environments where their patterns of habitat selection may be influenced by environmentally stochastic dynamics (Morris, 2001). My simulations include, therefore, the coexistence of two competing species and a shared predator living in a stochastic and capricious environment. Incorporating the strategic effects of predators is crucial because there is accumulating evidence that adaptive coevolutionary behavioural responses of predators and prey can have far-reaching implications to the stability and structure of ecological communities (e.g., Brown *et al.*, 1999), and to our interpretations of adaptive behaviors by prey species (Lima, 2002).

I begin with a brief review of contemporary habitat-selection theory, then evaluate differences between regulating vs. non-regulating stochasticity on habitat selection. The distinction is important because many stochastic processes are unlikely to alter the way in which populations are regulated. I use modified host-parasitoid equations to model and to simulate population

dynamics of habitat selectors across two trophic levels. I use the simulations to evaluate costs of coexistence between two 'prey' species and their shared habitat-selecting predator. I also use the simulations to assess preliminary patterns of community stability, as well as patterns of dispersal.

I assess the consequences of habitat selection on coexisting species, with special attention to the role that habitat-selecting predators play in promoting habitat separation of prey. I ask whether stochastic dynamics obfuscate our ability to measure competitive interactions between prey species, then explore whether an overlay of habitat-selecting predators helps to clarify or confound our understanding of prey competition. My approach is to first simulate simple two-trophic-level communities with known structure. I then shift gears to ask how likely it would be for a field biologist, encountering such a community, to properly diagnose the interactions among species. I conclude with a discussion of the role that habitat-selection theory can play in our general understanding of species abundance and distribution, and the costs of their coexistence.

Isodar theory

An ideal-free distribution (Fretwell and Lucas, 1970), where densities in different habitats are adjusted such that mean fitness is the same in each, will occur whenever individuals select habitats that maximize their Darwinian fitness, and when they are free to occupy the habitats that they choose. One way to reveal such a distribution, and to measure the various interactions among species that influence it, is to plot the densities in adjacent habitats (the habitat isodar, Morris, 1987, 1988, 1989). Imagine, for example, that two competing species with discrete intervals of reproduction vary in their preferences for two adjacent habitats (distinct habitat preferences, Pimm and Rosenzweig, 1981; Morris, 1988). The dynamics for species 1 can be modelled by a pair of habitat-specific discrete-logistic equations,

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

and

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

where N_{ij} is population size of species i in habitat j at times t and $t + 1$, r is the intrinsic rate of population increase, K is carrying capacity, and α is the *per capita* competitive effect of species 2 on species 1 in habitat j . For an ideal-free distribution, fitness is identical in both habitats, and dropping the subscripts for species,

$$\frac{N_{B(t+1)} - N_{B(t)}}{N_{B(t)}} = \frac{N_{A(t+1)} - N_{A(t)}}{N_{A(t)}}. \quad (3)$$

Substituting Equations (1) and (2) into Equation (3) yields the linear isodar

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

and similarly for species 2 (Morris, 1988, 1989, 1999a, b, 2003b; Morris *et al.*, 2000a, b). Equation (4) can be solved by multiple regression. The competitive interactions, as well as the degree of density-dependent habitat selection, are revealed by the corresponding regression coefficients (Morris, 1989, 1999a; Rodríguez, 1995; Morris *et al.*, 2000).

Regulating vs. non-regulating stochasticity

Populations, and their optimum habitat distributions, are influenced by a variety of deterministic and stochastic processes. Random variation in individual survival and reproduction, particularly at small population sizes, can affect the probabilities of local population persistence (demographic stochasticity). At larger scales, a variety of disturbances effect changes in reproductive potential and carrying capacity, and play a significant role in the regulation of populations by altering their size and dynamics (May, 1973; Hassell, 1978; Turchin, 1999, and many others). These environmentally stochastic effects are usually incorporated into (closed) models of population dynamics as exogenous random variables influencing either the population's growth rate, or its carrying capacity (e.g., Leigh, 1975; Hutchinson, 1978).

At the scale of habitat selection, however, populations are open to dispersal that allows many additional stochastic processes to influence local dynamics. Dispersal, for example, may depend not only on regional population dynamics, but on the spatial context within which habitats are embedded. Immigrants may be pumped into an area from source habitats, or emigrants may leave to occupy nearby sinks. Predators may 'spill-over' from rich elements in the landscape (Łomnicki, 1978; Holt, 1984, 1985; Oksanen, 1990; Oksanen *et al.*, 1992) and reduce the densities of prey species occupying otherwise 'safe' habitats. Competitors, and other species in the larger ecological community, will behave, and be influenced, similarly. Some of these processes will undoubtedly influence carrying capacity, alter the feedback of density on population growth, and thereby population regulation. But many other processes will simply alter a population's size without changing the relationship between growth rate and carrying capacity (non-regulating stochasticity). Regulating

stochasticity, with potential to change a habitat's maximum growth rate and carrying capacity, will also alter the pattern of distribution by habitat-selecting individuals (the isodar changes, Fig. 1). Non-regulating stochasticity will alter local densities, but not the underlying habitat isodar. One might presume, therefore, that regulating stochasticity may 'obscure' our ability to detect habitat selection, and to measure interactions among competing species. Accordingly, I incorporate both forms of stochasticity into simulations of habitat selection. My objective is to determine how trophic interactions and stochasticity affect our ability to understand the competitive coexistence of habitat-selecting prey. The habitat-selection response is assumed to operate on a faster time-scale than population dynamics. Thus, the stochastic influences do not include autocorrelated temporal patterns that are crucial in complementary studies evaluating whether we can detect the stochastic influences themselves (Lundberg and Ripa, 2002).

Habitat selection of two prey species sharing a common predator

Imagine two annually reproducing prey species sharing a common parasitoid 'predator' with a type II (Holling, 1959) functional response. Imagine further that we wish to follow the time-specific dynamics of all three species in two habitats. The population size of species 1 in habitat A can thus be calculated as

$$N_{1(t+1)A} = \lambda_{1A} N_{1tA} \left(\exp \left[-\frac{r_{1A}}{K_{1A}} \{N_{1tA} + \alpha_{12A} N_{2tA}\} - \frac{a'_A T P_{tA}}{1 + a'_A T_{h1A} N_{1tA}} \right] \right) \quad (5)$$

where λ_{1A} is the species' maximum net reproductive rate in habitat A , r is the instantaneous maximum growth rate, K is carrying capacity, α is the competitive effect of species 2 in habitat A , a' is the attack rate (e.g., area searched) of the predator (parasitoid), T is the total time that the predator spends foraging (1 year if set equal to unity), P is the number of predators, and T_h is the predator's handling time (Comins and Hassell, 1976; Hassell, 1978). The predator's dynamics can be calculated as

$$P_{(t+1)A} = c_{1A} N_{1tA} \left(1 - \exp \left[-\frac{a'_A T P_{tA}}{1 + a'_A T_{h1A} N_{1tA}} \right] \right) + c_{2A} N_{2tA} \left(1 - \exp \left[-\frac{a'_A T P_{tA}}{1 + a'_A T_{h2A} N_{2tA}} \right] \right) \quad (6)$$

where c is the number of predator offspring produced by each individual of prey species i in habitat j .

Equations (5) and (6) assume that the presence of a second prey species has no influence on the predator's effect on prey species 1. The assumption implies

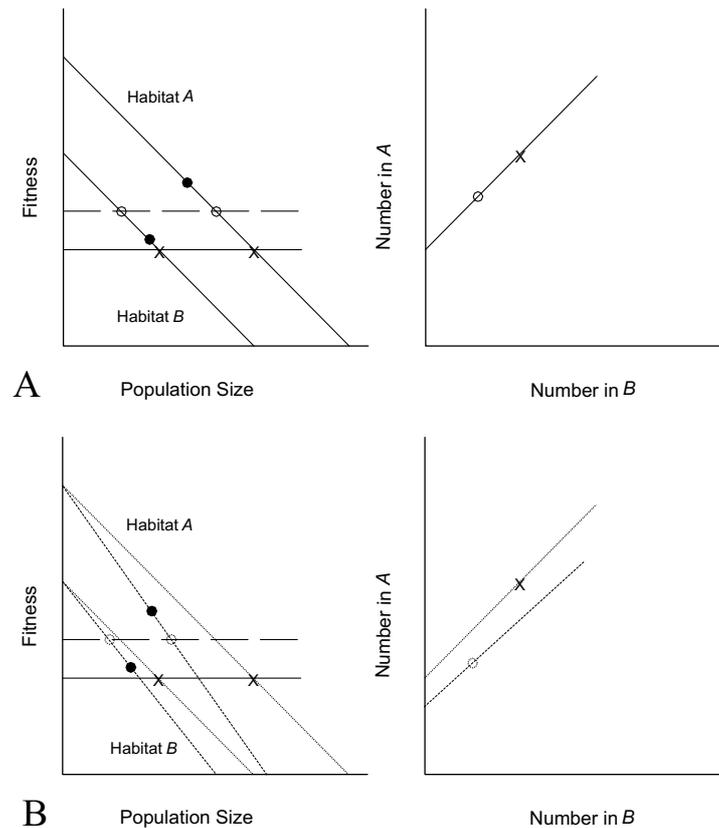


Figure 1. An illustration of the differences between non-regulating (A) and regulating stochasticity (B) on density-dependent habitat selection. Negatively sloped lines in the left panels represent caricatures of fitness declining in two different habitats. At time zero, the density in each habitat is assumed to be at an ideal-free distribution (IFD, equal fitness in both habitats, solid horizontal line marked with X). In (A) non-regulating stochasticity reduces population size in both habitats in the same direction, but to different degrees (solid circles). Individuals must move from habitat B where fitness is low to habitat A (where fitness is higher) to achieve a new IFD (dashed horizontal line, open circles). Individuals would flow in the opposite direction toward habitat B for an equivalent increase in population sizes (D.W. Morris *et al.*, unpublished data). The resulting habitat isodar, a line along which fitness is equal in both habitats at different densities, is plotted in the right panel. Both IFDs fall on the same isodar. Regulating stochasticity (variation in carrying capacity) is depicted in (B). The reduction in carrying capacity reduces population sizes further, and overall population size declines. The joint densities representing two different ideal-free distributions now fall on different isodars (right panel). Similar results for each scenario would apply to population increases. The habitat with the initially higher fitness, and thus the direction of dispersal to re-achieve an ideal distribution, will depend on the relative increases and declines in both forms of stochasticity.

that the predator is capable of handling both prey species simultaneously and independently. Ecologists are likely to have difficulty imagining such a predator. The image becomes more probable, however, if the coexisting prey

species tend to occupy different microhabitats (aided, perhaps, by their competitive interaction). Thus a predator, that allocates its search across the two major habitats, will encounter, and handle, each prey species independently. Regardless, use of one patch implies reduced use of others and a ‘two-resource disk equation’ may be a more appropriate model for habitat-selecting predators and prey. Preliminary simulations using such an equation (where the denominator of the functional response (Equation (5)) is expanded to $[1 + a'_A\{T_{h1A}N_{1tA} + T_{h2A}N_{2tA}\}]$ yield results comparable to those revealed from models of independent prey (Equations (5) and (6)).

I used Equations (5) and (6) to calculate the expected population sizes at time $t + 1$ for each species in each habitat. The general protocol of the simulations proceeded as follows: Step 1: At time t the habitats were colonized either by both prey species, or both prey plus their predator. Step 2: Individuals of all species included in the simulation then attempted to equalize their fitness in the two habitats. Step 3: Population density was adjusted at random. Carrying capacity either remained constant (simulations with only non-regulatory stochasticity), or was also adjusted at random (simulations with both regulating and non-regulating stochasticity). Step 4: The populations grew according to Equations (5) and (6). The simulation then looped back to step 2 and repeated all subsequent steps. The life history of each species was thus composed of discrete periods of reproduction followed by dispersal in an environment with ‘annual’ pulses of stochasticity.

I mimicked non-regulating stochasticity by allowing current population size of each prey species to fluctuate. Current density was multiplied by a normally distributed random variable with mean of zero (typical values ranged from -0.3 to $+0.3$). I mimicked regulating stochasticity similarly by allowing the carrying capacity of each prey in each habitat to vary in the same way (typical values ranged between -0.1 and $+0.1$). The simulations highlight differences in perspective between pure theory where carrying capacity is treated as a constant, and pure field biology where the objective is to estimate carrying capacity assuming that it is free to vary. Stochastic effects for each species and habitat varied independently, but were constrained such that the effects in both habitats (but not for both species) were in the same direction (i.e., either increasing or decreasing population size or carrying capacity, I assumed that stochastic influences operated at a large enough spatial scale to influence populations in each habitat similarly, but that the magnitude of the influence was free to vary). Stochastic influences on predators were assumed to be transmitted through those acting on prey.

I repeated the calculations of population size under the current regime of stochasticity to determine the sizes of each species expected at time $t + 2$ should the environment remain the same. I then calculated a prey individual’s expected fitness in each habitat, as $(N_{t+2} - N_{t+1})/N_{t+1}$, and similarly for the

predator. My estimate of fitness assumes that individuals will assess their fitness options in each habitat based on the conditions experienced during their lifetime. Other measures of fitness might be more appropriate (Kokko and Sutherland, 1998; Brommer *et al.*, 2000), and especially so if there is temporal autocorrelation in the stochastic effects (e.g., Lundberg and Ripa, 2002). Geometric-mean fitness (e.g., Levins, 1968; Boyce and Perrins, 1987; Morris, 1992; Holt and Barfield, 2001), for example, is likely to be a more accurate estimate of fitness in temporally variable environments. But it is unclear whether an individual's behavioral repertoire is sophisticated enough to key on the differences in multiplicative effects that would accrue in different habitats. For my purposes, which allow individuals to equalize their fitness in two habitats, use of a more complicated fitness variable would appear unnecessary because 1, the direction and limits of stochastic variation in both habitats are identical, and 2, there is no autocorrelation in the stochastic effects.

The algorithm raises an interesting question. Faced with stochastic, uncorrelated variation, does a winning strategy respond to current differences in fitness between habitats, or to the long-term average? We can answer the question by comparing the algorithm's habitat-selection game to sequential tosses of a perfectly balanced coin. The objective is to predict whether each successive toss will be heads or tails. A winning strategy must yield equal odds for heads and tails, but there are many possible and equivalent strategies that produce such an outcome. Yet for any short series of tosses the ratio of heads to tails is likely to be biased. A strategy using a rule-of-thumb that calls heads only after heads are tossed will be closer to the real ratio, and will tend to defeat a strategy using equal odds. A strategy of habitat selection where dispersal equalizes fitness by tracking varying carrying capacities distributed symmetrically around their mean value will be equivalent to one that imagines a static K . But a tracking strategy wins in the short-term when stochastic variation biases carrying capacity away from its long-term mean value.

After calculating expected fitness values in each habitat, I allowed a single individual of a randomly-chosen species to move to the habitat of higher fitness, then recalculated its expected fitness in each habitat at $t+2$ as above. If the individual could improve its fitness, it was allowed to remain in the new habitat, otherwise it would return to the original. Each of the other two species were then allowed to do the same before another random species assignment was made for habitat selection. The simulation stopped when all three species attained an ideal-free distribution (majority of cases), when each species had achieved its own ideal-free distribution on at least 10 different occasions, or when 250 movement iterations (750 individual movements [allowed each individual to move at least twice]) were completed. I classified the resulting outcomes as either ideal free (IFD) or non-ideal free (non-IFD) distributions even though it is unclear whether the non-IFD states were converging toward a

final IFD. The distinction, though arbitrary, can nevertheless classify the likelihood that a given simulation will readily achieve a true ideal-free distribution.

Many other authors have investigated spatial and temporal variation in stochastic environments where individuals migrate among populations (e.g., as cited in Engen *et al.*, 2002). My approach differs in that dispersal between habitats depends on density and functions as an adaptive behavior that equalizes fitness in each.

I restricted my analyses to a sub-set of the possible scenarios of species coexistence and habitat selection among the three species. I searched first for general parameter values that would allow each species to persist in at least one of the habitats for 1050 generations, and used these to describe long-term patterns in population size. I then ran a series (eight) of shorter 250-generation simulations to assess the relative roles of habitat selection on competition and predation, with and without regulating stochasticity, for pairs of prey species that possessed distinct preferences for the two different habitats. The simulations explored the complete set of possibilities among the presence and absence of competitors, predators, and regulating stochasticity. All simulations included non-regulating stochasticity. I assumed a trade-off between competition and predation risk, a scenario that should be common in nature. The inferior competitor imposed a higher handling time on the predator than did the most effective competitor. Each prey species was always assumed to impose higher handling costs on the predator in the prey's preferred habitat, than in its alternative habitat. Initial densities of the prey were set equal to each habitat's respective carrying capacity. I deleted the first 50 generations of each simulation to ensure that the community had attained dynamics free of initial conditions. I ran several other simulations to begin an assessment of the generality of the results. I report on those simulations (e.g., allowing the strong competitor to possess the greater handling time) only when it is relevant to do so.

I assessed costs of coexistence by calculating population sizes, dispersal, and patterns of overall dynamics and habitat selection. I contrasted differences in each metric when the prey species existed independently but with the predator present or absent, and when they competed in the presence and absence of the predator (parasitoid).

I evaluated the effect of competitors and predators on dispersal by calculating whether habitat selection resulted in pulses of dispersal (D.W. Morris *et al.*, unpublished data, Fig. 1), balanced migration between habitats (McPeck and Holt, 1992), or in source/sink dynamics (Pulliam, 1988). The term 'source-sink dynamics' implies habitats with positive vs. negative growth rates. In their place, I adopt the terminology of D.W. Morris *et al.* (unpublished data) where habitats are classified as either a donor (net emigration) or receiver (net immigration). I defined a habitat as a donor of emigrants if the net number of

individuals leaving the habitat at the end of the simulation exceeded the maximum number leaving in any single generation. I defined a habitat as a receiver similarly if the net number of immigrants exceeded the maximum number entering the habitat in one generation.

I searched for evidence of apparent competition by regressing the densities of one non-competing prey species reached in every generation against those of the other. Negative slopes in the presence of the predator, but not in its absence, would implicate apparent competition.

I assessed patterns of habitat selection both by examining overall mean population sizes in different habitats, and by isodar analysis. The isodar analyses are especially interesting because they allow me to assess the likelihood that field studies will be able to capture the crucial dynamic processes that influence species coexistence among habitats. I restricted isodar analyses to those generations when both habitats were occupied. Inclusion of zero densities can bias the isodar calculations because they may not yield a uniquely determined density in the alternative habitat (multiple possible densities below the isodar intercept, Fig. 1).

Results

All species frequently achieved ideal-free habitat selection

Even with stochastic dynamics and differences between habitats in the density of predators, the vast majority of prey distributions reached an ideal-free state where no individual could improve its fitness by dispersing to a different habitat (Table 1). All distributions without predators reached an ideal-free state. The presence of predators made truly ideal-free distributions more difficult to attain and caused habitat distributions to shift toward non-IFD states (Table 1).

Do the non-IFD communities really represent an inability to achieve ideal-free distributions, or are they simply an aberration from a conservative algorithm that limited movement? I addressed this question by repeating the simulation with non-competing prey living with predators in an environment without stochastic variation in K (simulation 2). I classified the joint distribution of the three species as non-IFD if an IFD state was not reached after 500 dispersal events (1500 individual movement opportunities). Thirty-eight of the 200 generations did not attain an IFD. The result demonstrates that my original algorithm was indeed conservative (65 vs. 38 non-IFD distributions; 9 of the second simulation's IFD distributions were obtained beyond the original limit of 250 dispersal events). But the analysis also reiterates the conclusion that IFD distributions are much more difficult to achieve when prey coexist

Table 1. Most of the eight main simulations of density-dependent habitat selection between two prey species and their shared predator reached an ideal-free distribution

| Number and type of simulation | | | | IFD ^a | Non-IFD | Extinctions | | | Ghost ^b |
|-------------------------------|------------|--------------------------|-----------|------------------|---------|-------------|-------|----------------|--------------------|
| # | Competitor | Regulating stochasticity | Predators | | | Prey1 | Prey2 | Predator | |
| 1 | Absent | Absent | Absent | 200 | 65 | 0 | 0 | 0 | 2 |
| 2 | Absent | Absent | Present | 135 | | 3 | 52 | 0 | |
| 3 | Absent | Present | Absent | 200 | 73 | 0 | 0 | 0 | 1 |
| 4 | Absent | Present | Present | 127 | | 2 | 59 | 0 | |
| 5 | Present | Absent | Absent | 200 | 61 | 0 | 0 | 0 | 3 |
| 6 | Present | Absent | Present | 169 | | 6 | 71 | 8 | |
| 7 | Present | Present | Absent | 200 | 51 | 0 | 0 | 0 | 0 |
| 8 | Present | Present | Present | 149 | | 0 | 103 | 8 ^c | |

Prey extinctions occurred only in the presence of predators. All simulations ran for 250 generations. Data represent the final 200 generations only. Parameter values are as follows: $N_{1(0)A} = K_{1A} = N_{2(0)B} = K_{2B} = 200$, $N_{1(0)B} = K_{1B} = 150$, $N_{2(0)A} = K_{2A} = 175$, $P_{(0)A} = 12$, $P_{(0)B} = 15$, $\alpha_{12A} = 0.2$, $\alpha_{21B} = 0.25$, $\alpha_{12B} = 0.25$, $\alpha_{21A} = 0.3$, $\lambda_{1A} = \lambda_{2B} = 2.4$, $\lambda_{1B} = \lambda_{2A} = 1.2$, $d'_A = 0.009$, $d'_B = 0.008$, $T_{h1A} = 0.055$, $T_{h2A} = 0.05$, $T_{h1B} = 0.056$, $T_{h2B} = 0.06$, $T = 1$, $c_{1A} = c_{1B} = 0.75$, $c_{2A} = c_{2B} = 0.7$, regulating stochasticity = 0.1, non-regulating stochasticity = 0.3. ^aIFD = ideal-free distribution; ^bsimulations where each prey species occupied only its preferred habitat; ^ceach prey species went extinct only in its less-preferred habitat, the predator went extinct in its less-preferred habitat *B* 15 times, and became extinct in habitat *A* only once when prey competed in habitats with stochastic variation in carrying capacity.

with habitat-selecting predators, than when they coexist in predator-free communities.

Habitat extinctions of prey were common in the presence of predators

Equally notable was an increased frequency of local habitat extinctions when predators were present. The frequency of local habitat extinctions appeared to be higher for competing prey species than it was for prey that existed independent of one another (Table 1). With only one exception (the predator existing with competing prey with stochastically varying carrying capacities), each species went extinct only in its less-preferred habitat. Local habitat extinctions thereby reinforce habitat preferences, and result in increased species separation that can reduce, and when each species occupies only its preferred habitat, eliminate competitive interactions (the ghost of competition). Indeed, in six of the 11 instances where prey species 1 occupied only its preferred habitat (*B*), prey species 2 was also restricted to its preferred habitat (*A*). The inferior competitor (species 2), experienced far more local extinctions than the 'dominant' competitor, even though species 2 was allowed to compensate for reduced competitive ability through reduced predation (lower search time in its preferred habitat *B*, longer handling times). Thus, nested niches, where

species 1 used both habitats while species 2 occupied only its preferred habitat, were much more common than the ghost of competition. I caution readers that ‘patterns’ in extinction are specific to my choice of parameter values for the simulations. It would seem reasonable, however, to conclude that habitat-selecting predators can amplify prey habitat preferences, increase the frequency of local habitat extinctions, and thereby create communities structured on both nested niches and ghosts of competition.

Pulses of dispersal were associated with dramatic population fluctuations

Populations of the parasitoid predator and its prey, reflecting both non-regulating and regulating stochasticity, fluctuated dramatically in the two habitats (Figs. 2 and 3). Dispersal was pulsed as individuals flowed from high to low density habitats during periods of population increase, and in the reverse direction during population decline (e.g., D.W. Morris *et al.*, unpublished data, Figs. 1 and 4). In my 1000-generation simulations, dispersal by the prey species most susceptible to predation (1), and the predator, occurred during nearly all generations (Fig. 4). The less susceptible prey species (2) was far less likely to disperse during any single interval of time (Fig. 4). The same overall pattern was maintained in the main set of eight different simulations (Fig. 5), but the relative numbers of dispersing prey varied significantly among treatments (four-way interaction among species, presence of competition and predation, and stochasticity; hierarchical loglinear analysis [data rounded to integers], *L. R.* $\chi^2_1 = 10.89$, $p = 0.001$). A sub-analysis based on only those treatments when predators were present detected significant two-way interactions (*L. R.* $\chi^2_7 = 70.25$, $p < 0.001$) where the number of dispersing individuals among species depended on whether the carrying capacity was constant or not (species \times stochasticity interaction, *L. R.* $\chi^2_2 = 11.47$, $p = 0.003$), and on whether competition was occurring or not (species \times competition interaction, *L. R.* $\chi^2_2 = 42.24$, $p < 0.001$). The total number of individuals of all species dispersing in constant vs. variable environments depended on whether the prey species competed or not (stochasticity \times competition interaction, *L. R.* $\chi^2_1 = 9.02$, $p = 0.003$).

Donor–receiver dynamics were common among ideal-free habitat selectors

Approximately one-half of the simulations resulted in net donor/receiver dynamics, even though all individuals were attempting to achieve an ideal-free distribution (Table 2). Dispersal was balanced between habitats in the remaining simulations. Even though donor/receiver dynamics were common, there was no obvious pattern related to the simulation treatments. It appears, instead, that the net flow of individuals from one habitat to another depends on

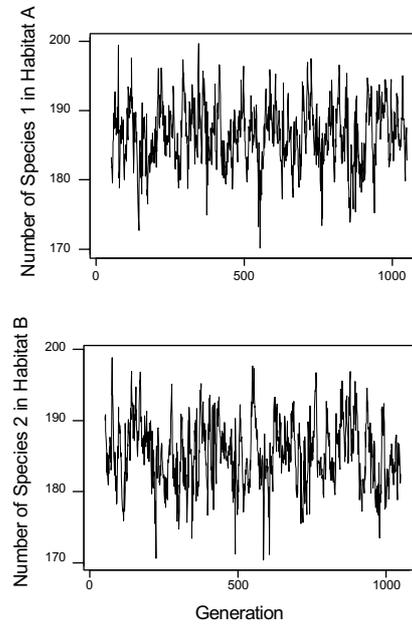


Figure 2. An example of dramatically fluctuating dynamics of model populations of two habitat-selecting prey species in their respective preferred habitats under non-regulating stochasticity, and without predators. Parameter values are as follows: $N_{1(0)A} = K_{1A} = N_{2(0)B} = K_{2B} = 200$, $N_{1(0)B} = K_{1B} = N_{2(0)A} = K_{2A} = 100$, $P_{(0)A} = 0$, $P_{(0)B} = 0$, $\alpha_{12A} = \alpha_{21B} = 0.6$, $\alpha_{12B} = \alpha_{21A} = 0.4$, $\lambda_{1A} = \lambda_{2B} = 2.4$, $\lambda_{1B} = \lambda_{2A} = 1.2$, $a'_A = 0.009$, $a'_B = 0.008$, $T_{h1A} = T_{h2A} = 0.025$, $T_{h1B} = 0.02$, $T_{h2B} = 0.03$, $T = 1$, $c_{1A} = c_{1B} = 0.75$, $c_{2A} = c_{2B} = 0.7$, regulating stochasticity = 0, non-regulating stochasticity = 0.3.

the stochastic history of each population and the community within which it is embedded. I confirmed this interpretation by two additional simulations with non-competing prey without predators in environments lacking regulating stochasticity. In one case the results were qualitatively identical to those in Table 2 (habitat A was a receiver for species 1 [net flow = -246], but a donor for species 2 [net flow = 54]), but in the other, they departed significantly (habitat A served as a donor for both prey species [102 and 322 net dispersers, respectively]).

There was no apparent competition between prey, but predators had major influences on patterns of prey population size

Regressions of total density of species 1 vs. that of species 2 (across generations within a single simulation) yielded only positive slopes (no apparent competition). One might argue, however, that negative feedbacks of predators on prey populations in the model communities might reflect lagged densities,

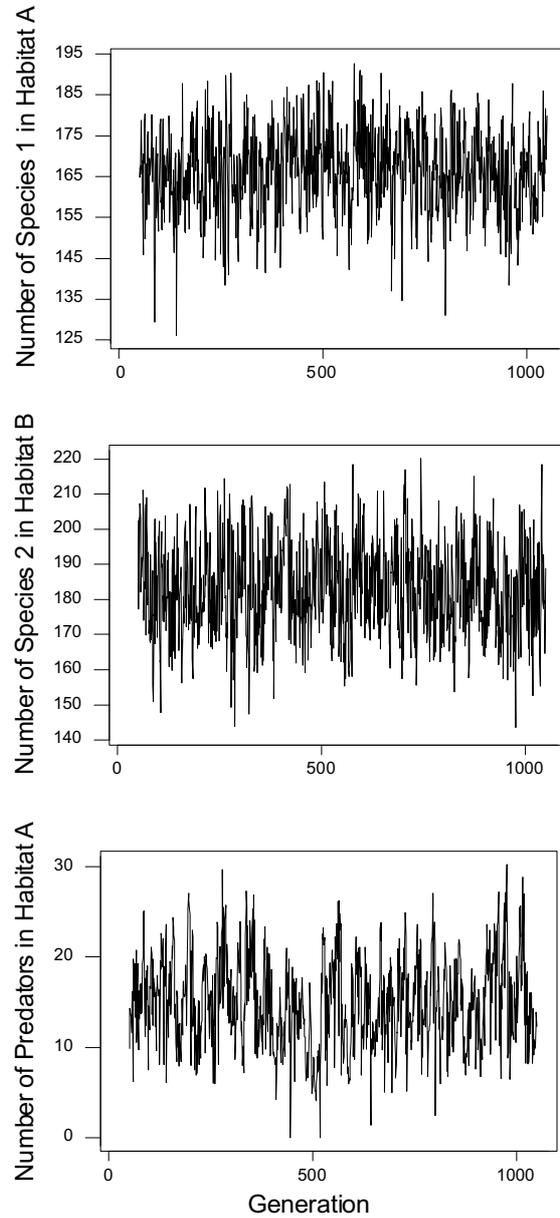


Figure 3. An example of the dramatically fluctuating dynamics of model populations of two habitat-selecting prey species and their parasitoid 'predator'. Parameter values are as follows: $N_{1(0)A} = K_{1A} = N_{2(0)B} = K_{2B} = 200$, $N_{1(0)B} = K_{1B} = N_{2(0)A} = K_{2A} = 100$, $P_{(0)A} = 12$, $P_{(0)B} = 15$, $\alpha_{12A} = \alpha_{21B} = 0.6$, $\alpha_{12B} = \alpha_{21A} = 0.4$, $\lambda_{1A} = \lambda_{2B} = 2.4$, $\lambda_{1B} = \lambda_{2A} = 1.2$, $a'_A = 0.009$, $a'_B = 0.008$, $T_{h1A} = T_{h2A} = 0.025$, $T_{h1B} = 0.02$, $T_{h2B} = 0.03$, $T = 1$, $c_{1A} = c_{1B} = 0.75$, $c_{2A} = c_{2B} = 0.7$, regulating stochasticity = 0.1, non-regulating stochasticity = 0.3.

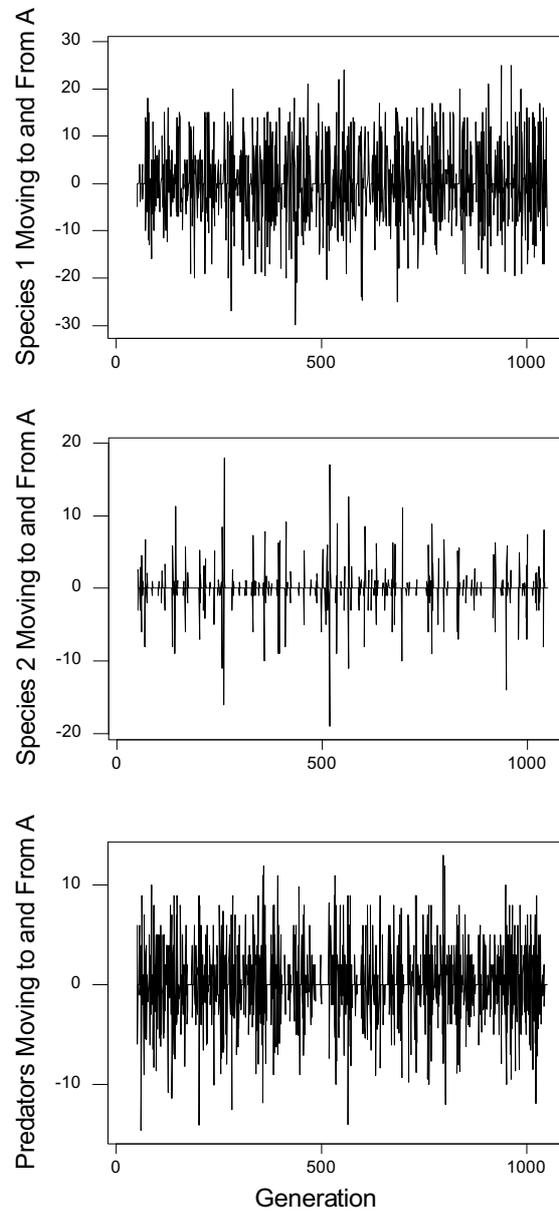


Figure 4. An example of pulsed dispersal by two habitat-selecting prey species and their parasitoid 'predator'. Negative values indicate immigration into habitat *A*, positive values correspond to emigration out of habitat *A*. Parameter values as in Figure 3.

rather than current ones. I tested for such an effect by regressing total population size of each prey species against the lagged density of its putative or real

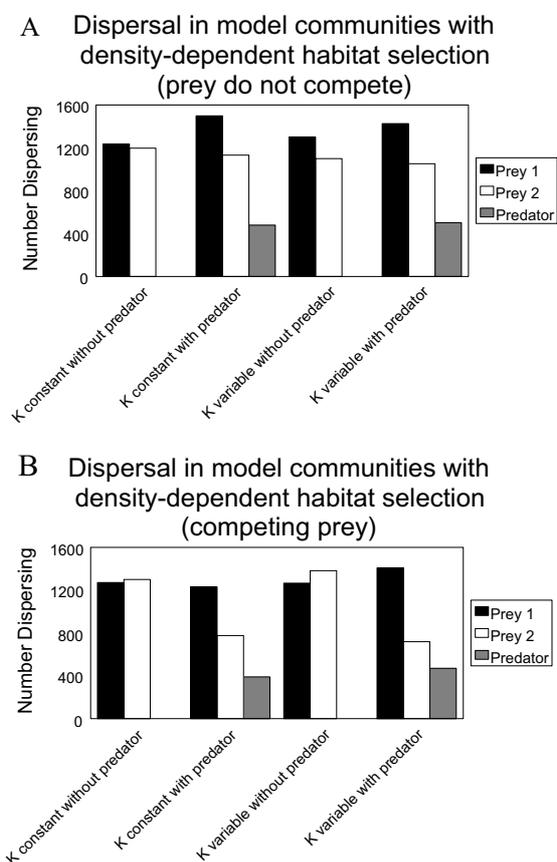


Figure 5. The total number of individuals dispersing from one habitat to another in eight different model communities. The number of dispersing individuals is summed over 200 generations.

competitor in the previous generation. I restricted the analysis to the four scenarios without stochastic variation in K (Table 1) to ensure that the results reflected only the possible effects of predation. Results in the presence of predators were identical to those in their absence. Total population sizes of each prey produced regressions (when significant, 11 of 12 cases) that had positive slopes with either current, or lagged density of the other prey species.

Yet it is clear (and unsurprising) that predators had major negative effects on prey density whether the prey competed or not (Fig. 6). Relative to predators, regulating stochasticity had imperceptible effects on mean population sizes. Ratios of prey population sizes in the two habitats changed dramatically in the presence of predators (Fig. 6). The mean sizes of both prey species were reduced dramatically in their less preferred habitats when subjected to

Table 2. Directional dispersal was a common outcome from many of the eight main simulations of density-dependent habitat selection between two prey species and their shared predator

| Type of simulation | | | Net dispersal to habitat A by species ^a | | |
|--------------------|--------------------------|-----------|--|---------------|---------------|
| Competitor | Regulating stochasticity | Predators | Prey 1 | Prey 2 | Predator |
| Absent | Absent | Absent | -33 (17 R) | 202 (20 D*) | |
| Absent | Absent | Present | 48.7 (23 D) | 28.7 (28) | 9.2 (23.1) |
| Absent | Present | Absent | -246 (-28 R*) | -0.00 (-16) | |
| Absent | Present | Present | 13.4 (21) | -27.9 (-18 R) | 12.7 (7 D) |
| Present | Absent | Absent | 54 (16 D*) | -11 (-16) | |
| Present | Absent | Present | -62.7 (-27 R) | -11.1 (-17) | -43.4 (-7 R*) |
| Present | Present | Absent | 130 (17 D*) | -101 (-19 R*) | |
| Present | Present | Present | 0.00 (31) | -4.2 (-42) | 26.1 (15.3 D) |

D = Donor, R = Receiver.

^aAppropriate maxima or minima of dispersal in a single generation are noted in parentheses.

*Large departures from single-generation values that yield clear evidence of donor/receiver regulation.

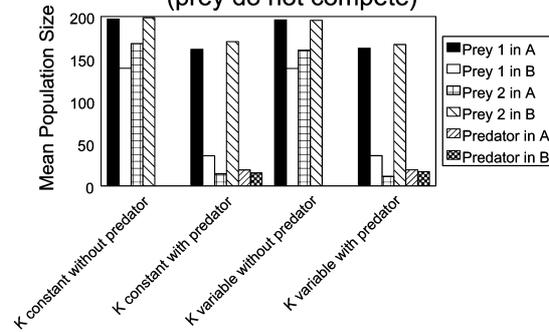
habitat-selecting predators. Even though the indirect effects of a shared predator did not create negative correlations in prey abundance, they did reinforce prey habitat selection.

Differences in prey distribution were also reflected in differences between isodars when predators were present compared to isodars when they were absent (Table 3). Some highly significant negative effects were revealed for competing prey in their preferred habitats, but the signs were opposite to those expected from isodar analysis. It is clear, nevertheless, that predators influence habitat selection of prey in a way that depends not only on the numerical response by predators, but also on their density-dependent habitat selection. Prey habitat choice can thereby be assumed to reflect not only the dynamic effects of shared predators (e.g., Holt, 1977, 1984; Holt and Lawton, 1994), but also short-term apparent competition (Holt and Kotler, 1987) driven by adaptive predator behavior.

Prey population sizes were reduced by competition

As expected, mean prey population sizes were less when prey competed with one another, than when their populations were regulated separately (Fig. 6). The reduced population sizes also resulted in more frequent local extinctions in the presence of habitat-selecting predators (Table 1). The effect of the predator depended on the identity of the prey species and its preferred habitat. The density of the inferior competitor was reduced proportionately more in its less preferred habitat than was that of the better competing prey species (Fig. 6), a

(A) Population sizes in model communities with density-dependent habitat selection (prey do not compete)



(B) Population sizes in model communities with density-dependent habitat selection (prey compete)

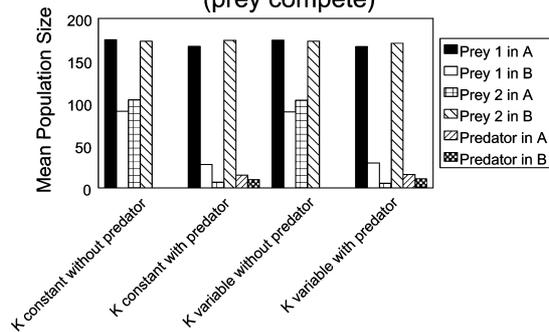


Figure 6. Mean population sizes of two habitat-selecting prey species and their habitat-selecting predator in eight different model communities. The mean is calculated across 200 generations. The two prey species have identical growth rates and carrying capacities in their preferred habitats ($\lambda = 2.4$, $K = 200$), identical growth rates in their less preferred habitats ($\lambda = 1.2$) but different carrying capacities in their secondary habitat choices ($K_{1B} = 150$, $K_{2A} = 175$). Predators are more efficient in habitat A ($a'_A = 0.009$) than in habitat B ($a'_B = 0.008$), and prey species 2 trades off poor competitive ability ($\alpha_{12A} = 0.2$, $\alpha_{12B} = 0.25$, $\alpha_{21A} = 0.3$, $\alpha_{21B} = 0.25$) for lower predation risk ($T_{h1A} = 0.055$, $T_{h1B} = 0.05$, $T_{h2A} = 0.056$, $T_{h2B} = 0.06$; $c_1 = 0.75$ in both habitats, $c_2 = 0.7$).

result that also caused a much higher rate of local habitat extinction in the inferior competitor (Table 1). The asymmetrical habitat-dependent competitive effect is especially intriguing because the same prey species traded off its lack of competitive ability in favor of a reduced risk of predation. High predator densities in habitat A reflected its greater search efficiency in that habitat, and the habitat's preference by the more valuable prey species (1). All things equal, increased density of species 1 in habitat A would increase the density of predators in that habitat where their influence on prey species 2 is greater than

Table 3. Summary of isodar analyses between two prey species with distinct preferences for two different habitats (analyses based only on prey, equations included; see Equation (4) for the procedure to calculate estimates of competition; values were calculated with more significant digits than recorded here). Signs of net competitive effects included for clarity

| Type of simulation | | Estimate of competition (actual value) | | | | |
|--|--------------------------|--|------------------|------------------|-----------------------|------------------|
| Competitor | Regulating stochasticity | Predators | $\alpha_{1,2,A}$ | $\alpha_{1,2,B}$ | $\alpha_{2,1,A}$ | $\alpha_{2,1,B}$ |
| Absent | Absent | Absent | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| $N_{1,A} = 158.2 + 0.28N_{1,B}; R_{\text{adj}}^2 = 0.996, F_{1,198} = 54104, p = 0.000$ | | | | | | |
| $N_{2,B} = 158.4 + 0.24N_{2,A}; R_{\text{adj}}^2 = 0.997, F_{1,198} = 67270, p = 0.000$ | | | | | | |
| Absent | Absent | Present | 0.19 (0) | 3.34 (0) | 0.27 (0) | 5.06 (0) |
| $N_{1,A} = 319.5 + 0.29N_{1,B} - 0.97N_{2,B} + 0.19N_{2,A}; R_{\text{adj}}^2 = 0.91, F_{3,143} = 467.8, p = 0.000$ | | | | | | |
| $N_{2,B} = 299.7 + 0.17N_{2,A} - 0.86N_{1,A} + 0.27N_{1,B}; R_{\text{adj}}^2 = 0.91, F_{3,143} = 350.2, p = 0.000$ | | | | | | |
| Absent | Present | Absent | -0.07 (0) | 0 (0) | 0 (0) | 0 (0) |
| $N_{1,A} = 164.3 + 0.31N_{1,B} - 0.068N_{2,A}; R_{\text{adj}}^2 = 0.32, F_{2,197} = 47.2, p = 0.000$ | | | | | | |
| $N_{2,B} = 164.4 + 0.19N_{2,A}; R_{\text{adj}}^2 = 0.2, F_{3,198} = 49.8, p = 0.000$ | | | | | | |
| Absent | Present | Present | -0.96 (0) | -0.79 (0) | -1.08 (0) | -0.94 (0) |
| $N_{1,A} = 10.5 + 0.96N_{1,B} + 0.76N_{2,B} - 0.96N_{2,A}; R_{\text{adj}}^2 = 0.91, F_{3,136} = 445.8, p = 0.000$ | | | | | | |
| $N_{2,B} = 20 + 1.14N_{2,A} + 1.07N_{1,A} - 1.08N_{1,B}; R_{\text{adj}}^2 = 0.86, F_{3,136} = 275.3, p = 0.000$ | | | | | | |
| Present | Absent | Absent | -0.19 (-0.2) | 0 (-0.25) | 0 (-0.3) | -0.23 (-0.25) |
| $N_{1,A} = 170.2 + 0.26N_{1,B} - 0.19N_{2,A}; R_{\text{adj}}^2 = 0.99, F_{2,197} = 12545.6, p = 0.000$ | | | | | | |
| $N_{2,B} = 170.6 + 0.23N_{2,A} - 0.23N_{1,B}; R_{\text{adj}}^2 = 0.99, F_{2,197} = 21420.9, p = 0.000$ | | | | | | |
| Present | Absent | Present | 45.2 (-0.2) | 0 (-0.25) | U ^a (-0.3) | 0.02 (-0.25) |
| $N_{1,A} = 349.7 + 0.02N_{1,B} - 1.03N_{2,B}; R_{\text{adj}}^2 = 0.94, F_{2,123} = 981.6, p = 0.000$ | | | | | | |
| $N_{2,B} = 330.4 - 0.91N_{1,A} + 0.02N_{1,B}; R_{\text{adj}}^2 = 0.94, F_{2,123} = 956.4, p = 0.000$ | | | | | | |
| Present | Present | Absent | 0.81 (-0.2) | 0.18 (-0.25) | 0.15 (-0.3) | 1.33 (-0.25) |
| $N_{1,A} = 140.2 + 0.37N_{1,B} + 0.18N_{2,B} - 0.30N_{2,A}; R_{\text{adj}}^2 = 0.36, F_{3,196} = 38.9, p = 0.000$ | | | | | | |
| $N_{2,B} = 150.2 + 0.25N_{2,A} + 0.15N_{1,A} - 0.33N_{1,B}; R_{\text{adj}}^2 = 0.33, F_{3,196} = 33.5, p = 0.000$ | | | | | | |
| Present | Present | Present | 0 (-0.2) | 0.16 (-0.25) | 0.3 (-0.3) | 1.13 (-0.25) |
| $N_{1,A} = 136.7 + 0.10N_{1,B} + 0.16N_{2,B}; R_{\text{adj}}^2 = 0.04, F_{2,94} = 3.11, p = 0.05$ | | | | | | |
| $N_{2,B} = 132.4 + 0.26N_{2,A} + 0.3N_{1,A} - 0.29N_{1,B}; R_{\text{adj}}^2 = 0.09, F_{3,93} = 275.3, p = 0.007$ | | | | | | |

^a U = unable to calculate.

the smaller number of predators in habitat *B*. Again, this indirect effect is likely to include components of both short- and long-term apparent competition.

Isodars produced valid estimates of competition in ‘constant’ environments without predators

Each simulation produced significant prey isodars (Table 3). Isodars calculated for environments lacking predators without regulating stochastic variation in prey carrying capacity generally yielded highly accurate estimates of competition. There was one major exception. When the two prey species competed, the isodars did not include the negative effect of the competing species in its preferred habitat.

Isodars yielded valid estimates of competition in ‘variable’ environments only when regulating stochasticity was included in the solution

Regulating stochastic variation in carrying capacity also produced isodars that failed to estimate accurate competitive interactions between species. This too is not surprising (recall Fig. 1). But isodars yielded incredibly accurate estimates of competitive interactions when I included values of stochastic carrying capacities in the multiple-regression solution (estimates: $\alpha_{12A} = -0.2$, $\alpha_{12B} = 0.26$, $\alpha_{21A} = 0.29$, $\alpha_{21B} = -0.25$; actual values: $\alpha_{12A} = -0.2$, $\alpha_{12B} = 0.25$, $\alpha_{21A} = 0.3$, $\alpha_{21B} = -0.25$; estimates from Equation (4), Appendix 1, Table 4).

Isodars did not detect competition between prey in the presence of habitat-selecting predators

Isodars, even when they included predator population sizes, did not detect competitive interactions between species (Table 3, Appendix 1, Table 4). Indeed, estimates of competition were frequently of impossible magnitudes and opposite in sign to actual competition between species. Was the ‘failure’ of isodars caused by non-IFD distributions? I answered this question by repeating the isodar analysis for competing prey coexisting with predators, but without regulating stochasticity (simulation 6). The IFD-only isodar for species 1 was virtually unchanged. The IFD-only isodar for species 2 included only the negative coefficient for species 1 in habitat *A*. There appeared to be no competition in the presence of shared habitat-selecting predators even though multiple regressions always included significant predator effects.

Habitat preference of the predator was revealed by its linear isodar

Isodars consistently identified density-dependent habitat selection by the predator. Predator isodars were highly significant for every simulation that included predation (Appendix 1; Table 4, $R_{\text{adj}}^2 > 0.4$, $p < 0.001$ in each case).

Discussion

Several lessons emerge from the joint consideration of optimal habitat decisions by predators and their coexisting prey.

(1) Habitat-selecting predators did not produce any tendency for non-interacting prey species to exhibit negative influences on one another's population sizes (apparent competition). Predators altered prey distribution, but adaptive habitat selection by the prey appeared to destroy the ability of predators to force negative interactions. It is possible that the assumption of independent prey in Equations (5) and (6) eliminates indirect predator effects. I tested this possibility with a two-species version of the disk equation for a pair of non-competing species existing with their predator (analogous to simulation 2). The results were comparable to those of the independent-prey model. I repeated the analysis using a predator with a linear (type I) functional response. The results were, again, similar to those I report above.

Though there was no evidence for net 'numerical' apparent competition in any of the simulations, predators did effect behavioral shifts in prey habitat use that mimic those of competing species. Indeed, the habitat selection by prey that mirrors competition, effectively eliminates it (below). It is likely that the shifts in habitat preference reflect habitat-dependent numerical effects of predators (long-term apparent competition); Holt, 1977, 1984; Holt and Lawton, 1994) as well as adaptive habitat selection by prey in response to the predator's habitat choice (short-term apparent competition; Holt and Kotler, 1987).

(2) Isodar analysis failed to reveal the competition that occurs in the competitor's preferred habitat, even when carrying capacity was constant and predators were absent. Before becoming too critical of this 'failure', reflect for a moment on Equation (4). The regression coefficient used to estimate competition with species 1 in habitat *A* includes the isodar slope $((r_A/r_B)(K_B/K_A))$. The predicted regression coefficient is only 0.07 (0.23×0.3). That for species 2 in habitat *B* is even smaller. It is hardly surprising that significant regressions failed to include such a small combined effect. Thus, if you wish to evaluate all competitive interactions between species using isodars, you must design experiments with large differences between opposing habitats that are likely to produce large isodar slopes.

But readers should also note that detection of competitive interactions (even large ones) can be obscured by correlated responses in prey distribution effected by competition that occurs simultaneously and reciprocally in each habitat. Competition from species 2 in habitat *B* acts to reduce the density of species 1 in that habitat, while competition in habitat *A* acts to increase it (more individuals of species 1 in habitat *B*). A step-wise multiple regression may be unable to uncover the competition from 2 on 1 in habitat *A* because it is highly correlated (negatively) with that in habitat *B*. It will always be instructive, therefore, to examine the regression coefficients emerging from univariate regressions, and the correlations among variables included in the overall multiple regression analysis of competition.

(3) Isodars were similarly unable to estimate competition accurately when carrying capacities varied stochastically through time. The lesson: Conduct experiments at a temporal and spatial scale that minimizes the possibility for stochastic variation to modify local carrying capacities. You could, of course, control for stochasticity with estimates of carrying capacity, but this will often be impossible, at least in natural settings. It is instructive to note, however, that the analysis including stochastically varying carrying capacities appeared to overcome the correlated responses in prey distribution that obscure competitive interactions.

(4) By far the most intriguing results were those of the isodar analyses assessing competition when predators distributed themselves across the same habitat boundaries in an ideal-free manner. The analyses demonstrated that even when we include predator densities, strategic predator behavior destroys our ability to measure competitive interactions between prey. Stochastic variation in carrying capacity similarly limits isodar analysis, though competition emerges when we include the stochastic effects.

Look again at Figure 6. Predators always had a greater effect on prey population size, and habitat distribution, than did competition between prey species. Moreover, the predator's main influence occurred in each prey species' secondary habitat. Thus, a high number of each prey species living in their preferred habitat maintained relatively high predator populations that had a disproportionate effect on the more susceptible (lower handling time) prey species.

The predator's effect on prey distribution appears driven by its high search efficiency in habitat *A*. Prey species 2 maintained lower numbers in its secondary habitat (*A*) than did prey species 1 (in habitat *B*), even though the carrying capacity was higher for species 2. When predators were absent, competition was mediated by large numbers of prey species in secondary habitats. Habitat overlap with each competitor was high. When predators were present, habitat overlap between prey was greatly reduced, and the relative preference of the two prey species for secondary habitat choices was reversed

(Fig. 6). The important role of searching efficiency was confirmed from comparable results obtained from simulations based on linear (type I, zero handling time) functional responses (not illustrated).

With the parameter values I used here, the predator makes its living by feeding on the common prey species in each habitat. Encounter rates with predators that depress prey fitness are high in both habitats, but reproductive potential is much lower in secondary, than in primary, habitat. Fitness, already hovering near replacement rates ($\lambda = 1.2$) is depressed even more by abundant predators. Both prey species avoid their secondary habitats. Avoidance is disproportionately biased for species 2 because the predator is most efficient at finding prey in species 2's secondary habitat (*A*).

The predator's keystone effect jumps to life in Table 1. Whenever predators are present, they change the structure of the prey community. When predators are absent, prey occupy both habitats. When predators are present, prey often coexist with nested niches (predominately where prey species 1 exists in both habitats while prey species 2 exists only in its preferred habitat), and occasionally, as ghosts of competition (each prey species in only its preferred habitat). The predator acts not only as the keystone species in this simple three-species web, but is also its ecological wizard. The competition that we so readily observe between the two prey species vanishes when the predator weaves its magic. Prey populations are forced toward occupying their preferred habitats. As they do so, the ghost of competition eliminates their competitive interaction. Habitat selection by the consumer hides the light of competition within its predatory shadow. True, the interpretation is based on a very limited range of parameter values, and one may wonder how often predators can eclipse competition between prey. Recall my purpose. When you encounter a persistent community consisting of two coexisting competitors that share a habitat-selecting predator, can you measure the competitive interaction by censusing the populations in the field? The answer: no. But isodars did not fail to find competition; the predator hid it from their view. Be wary, fellow ecologists. Do not be duped by the competitor's eclipse. It is not magic. Remove the predator and you illuminate competition between prey.

The simulations and isodar analyses illustrate that we may often gain insights from output that will otherwise surprise us. We should suspect stochastic or predator-induced effects, for example, whenever isodars for putative competitors suggest positive interactions (apparent habitat mutualists). We should similarly be suspicious of any isodar solution that yields large estimates of species interaction. When such isodars emerge, we should attempt to evaluate whether the interaction has been modified by other species, or by stochastic variation.

Nevertheless, isodars are likely to be of greatest utility when used with controlled manipulative experiments. These experiments will be most effective

when designed to assess habitat selection of single species, top predators, or to measure species interactions within a single trophic level. What are we to do, then, with isodars that have attempted to assess competitive interactions and coexistence between prey in systems with several known predator species? Habitat choices by lemmings living in dry hummock and moist tundra habitats, for example, have been used to not only infer interactions between species, but also their competitive ghost, and habitat's role in population dynamics (Morris *et al.*, 2000a). Though numerous predators key on lemmings, especially when lemming numbers are high, virtually all have foraging ranges much larger than the spatial scale of the sedge-hummock contrast used in the isodar analysis. Thus, the habitats exploited by the lemmings correspond to different foraging patches of individual predators whose optimal strategy is to feed in each patch until they yield the same harvest rate (e.g., Charnov, 1976; Brown, 1988). It is thereby possible that isodars reveal valid interpretations of prey interaction across small spatial and temporal scales, such as those used in the lemming study. Studies over longer intervals, or over more extensive scales, may frequently include data with different densities of predators whose non-linear foraging behavior could produce far more complicated isodars (e.g., Brown, 1998). While I endorse the general call for ecologists to expand their interests to larger scales than classic experiments, I also caution readers to ensure that the scale they choose is appropriate for the processes causing pattern. Such a rule would seem to be especially crucial for isodar and habitat analysis.

In my models, I allowed the cost of competitive coexistence to be 'balanced' by a reduced cost of predation. Is such an effect necessary for species coexistence? I assessed this possibility by repeating many of the simulations where species 1, the superior competitor, was also more difficult for the predator to process (higher handling time in each habitat than that for species 2). I have not analyzed these models in the same detail as those for trade-offs, but it appears that general patterns in the isodars, and in species coexistence, remain. Thus, while it would seem reasonable that prey species trade-off competitive ability and susceptibility to predation, such a trade-off is unnecessary to permit their continued coexistence as long as the predator itself possesses a clear habitat preference (e.g., as by higher search efficiency in one habitat than in the other).

The simulations also shed considerable light on our understanding of habitat and stochasticity on dispersal by density-dependent habitat selectors. When sub-populations inhabiting different habitats experience different population growth rates and carrying capacities, fitness can be equalized only by pulses of dispersal that flow in different directions following periods of population growth and decline (D.W. Morris *et al.*, unpublished data). The net flux of individuals, and whether population dynamics produce donor and receiver

habitats, depends critically on the pattern of stochastic variation in population densities. My simulations, for example, allowed each species to experience independent stochastic effects, constrained only by a requirement that stochasticity was in the same direction in both habitats (but could be in different directions for each prey species). Different forms of stochasticity, including temporal and spatial autocorrelation, would produce different forms of pulsed dispersal. Nevertheless, the key point remains that ecologists studying donor–receiver dynamics might frequently be misled into rejecting ideal-free habitat selection. The problem becomes more acute as we add trophic dynamics. Stochastically linked pulses of dispersal by prey are translated into the adaptive habitat choices and dynamics of their shared predator.

Finally, the simulations add to our understanding of the role of habitat selection on species coexistence. As a case in point, Grand (2002) demonstrated that adaptive habitat selection promotes species coexistence even when competing species rank habitats similarly with respect to their productivities and predation risk, provided that each species is more vulnerable to predation in a different habitat. Others (reviewed by Grand) have shown how habitat selection enhances coexistence when each species is competitively superior in a different habitat, when they differ in which habitat possesses a higher risk of predation, and when species trade-off competitive ability for reduced predation risk. My approach has been somewhat different. I built simulations that allowed the prey species to coexist independent of the predator, then asked what the predator’s effect was on habitat-dependent patterns of coexistence. The analyses of this dynamic predator–prey habitat-selection game demonstrate that adaptive habitat choices by predators alter habitat patterns of prey density that can complicate our ability to measure underlying processes of coexistence. While some may despair at the added complexity, optimists will be encouraged by the ability of our models of habitat selection to measure and interpret processes of species coexistence. We can, with appropriate caution, use adaptive behaviors of habitat selection to detect the relative quality of habitats to both predators and prey, and to measure the interactions among coexisting species. Field biologists know when and where to find species because patterns of abundance and distribution emerge from strategic behaviors that reflect underlying processes of coexistence.

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Appendix 1

Table 4. Stepwise multiple regression solutions for the isodar analyses between two prey species with distinct preferences for two different habitats. Predator isodars are in parentheses

| Type of simulation | | |
|---|--------------------------|-----------|
| Competitor | Regulating stochasticity | Predators |
| Absent | Absent | Absent |
| $N_{1A} = 158.2 + 0.28N_{1B}; R_{\text{adj}}^2 = 0.996, F_{1,198} = 54104, p = 0.000$ $N_{2B} = 158.4 + 0.24N_{2A}; R_{\text{adj}}^2 = 0.997, F_{1,198} = 67270, p = 0.000$ | | |
| Absent | Absent | Present |
| $N_{1A} = 267.3 + 0.27N_{1B} - 0.68N_{2B} + 0.17N_{2A} + 0.59N_{PB} - 0.49N_{PA};$ $R_{\text{adj}}^2 = 0.95, F_{5,141} = 612.2, p = 0.000$ $N_{2B} = 311.6 + 0.19N_{2A} - 0.95N_{1A} + 0.29N_{1B} + 0.15N_{PB};$ $R_{\text{adj}}^2 = 0.9, F_{4,142} = 318.6, p = 0.000$ $(N_{PA} = 5.5 + 0.82N_{PB}; R_{\text{adj}}^2 = 0.75, F_{1,191} = 580.7, p = 0.000)$ | | |
| Absent | Present | Absent |
| $N_{1A} = -0.6 + 0.28N_{1B} + 0.99StocN_{1A} - 0.25StocN_{1B};$ $R_{\text{adj}}^2 = 0.998, F_{3,196} = 34039.6, p = 0.000$ $N_{2B} = 0.31 - 0.24N_{2A} + 0.99StocN_{2B} - 0.22StocN_{2A};$ $R_{\text{adj}}^2 = 0.998, F_{3,196} = 40145.3, p = 0.000$ | | |
| Absent | Present | Present |
| $N_{1A} = 0.07 + 0.8N_{1B} + 0.58N_{2B} - 0.72N_{2A} + 0.1N_{PA} + 0.21StocN_{1A};$ $R_{\text{adj}}^2 = 0.95, F_{5,134} = 518.4, p = 0.000$ $N_{2B} = 12.7 + 0.9N_{2A} + 0.78N_{1A} - 0.8N_{1B} - 0.14N_{PA} + 0.25StocN_{2B};$ $R_{\text{adj}}^2 = 0.92, F_{5,134} = 322.3, p = 0.000$ $(N_{PA} = 4.8 + 0.8N_{PB}; R_{\text{adj}}^2 = 0.76, F_{1,138} = 442.8, p = 0.000)$ | | |
| Present | Absent | Absent |
| $N_{1A} = 170.2 + 0.26N_{1B} - 0.19N_{2A}; R_{\text{adj}}^2 = 0.99, F_{2,197} = 12545.6,$ $p = 0.000$ $N_{2B} = 170.6 + 0.23N_{2A} - 0.23N_{1B}; R_{\text{adj}}^2 = 0.99, F_{2,197} = 21420.9,$ $p = 0.000$ | | |
| Present | Absent | Present |
| $N_{1A} = 3331.3 + 0.04N_{1B} - 0.94N_{2B} + 0.18N_{PB}; R_{\text{adj}}^2 = 0.96,$ $F_{3,122} = 907.1, p = 0.000$ $N_{2B} = 334.8 + 0.04N_{2A} - 0.89N_{1A} + 0.19N_{PA}; R_{\text{adj}}^2 = 0.95,$ $F_{3,122} = 802.9, p = 0.000$ $(N_{PA} = 9.0 + 0.60N_{PB}; R_{\text{adj}}^2 = 0.42, F_{1,191} = 137.8, p = 0.000)$ | | |

Table 4. (Continued)

| Type of Simulation | | |
|--|--------------------------|-----------|
| Competitor | Regulating stochasticity | Predators |
| Present | Present | Absent |
| $N_{1A} = -1.97 + 0.27N_{1B} + 0.07N_{2B} - 0.20N_{2A} + 0.98StocN_{1A}$ $-0.24StocN_{PB}; R_{adj}^2 = 0.998, F_{5,194} = 22967.3, p = 0.000$ $N_{2B} = 1.37 + 0.24N_{2A} + 0.07N_{1A} - 0.25N_{1B} + 0.97StocN_{2B}$ $-0.21StocN_{2A}; R_{adj}^2 = 0.998, F_{5,194} = 24643.2, p = 0.000$ | | |
| Present | Present | Present |
| $N_{1A} = 13.3 + 0.18N_{1B} - 1.33N_{PA} + 1.55N_{PB} + 0.90StocN_{1A}$ $-0.18StocN_{1A}; R_{adj}^2 = 0.89, F_{5,91} = 163.0, p = 0.000$ $N_{2B} = -0.6 - 0.16N_{1B} - 1.45N_{PB} + 1.38N_{PA} + 0.89StocN_{2B};$ $R_{adj}^2 = 0.93, F_{4,92} = 302.2, p = 0.000$ $(N_{PA} = 7.02 + 0.64N_{PB}; R_{adj}^2 = 0.53, F_{1,87} = 99.6, p = 0.000)$ | | |

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